# SEARCHING FOR THE BIOLOGICAL BASIS OF HUMAN MENTAL ABILITIES

## THE RELATIONSHIP BETWEEN ATTENTION AND INTELLIGENCE STUDIED WITH P3

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an academic essay in Social Sciences

Doctoral Thesis

to obtain the degree of doctor
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by

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# Contents

# CHAPTER 1

## GENERAL INTRODUCTION

During the past few decades enormous progress in our knowledge about brain functioning has been made. The application of several complementary methods, such as single cell recordings, functional brain imaging, electroencephalography or neuropsychological investigation of focal brain damages helped us to better understand how information is gathered and later processed within the brain as well as how the behavioral response to stimulation is determined. Now, we understand better how the brain works and how it is related to our functioning at the psychological level much better than thirty years ago.

What is surprising, however, is that there is still a gap between theories which explain basic brain functions and those which are focused on individual differences in mental abilities, such as fluid intelligence. This term refers to the factor that influences performance in diverse forms of cognitive abilities, especially reasoning and novel problem solving. Fluid intelligence is thought to be responsible for individual performance in a broad variety of cognitive and learning tasks (Cattell, 1963). This gap is even more surprising considering that, for example, the attempt to relate measures of electrophysiological activity to measures of intellectual ability has a history almost as long as that of electroencephalography itself (Vogel and Broverman, 1964). What should be noted, is the consensus that human intelligence can be related to the anatomical structures and physiological functions of the nervous system, and psychologists often refer to the brain as the basis for, or substrate of, intelligence (Deary and Caryl, 1997). One of the reasons underlying this problem is that fluid intelligence is a very complex psychological phenomenon that cannot be easily understood in terms of properties of nerve cells and brain circuitry. As it was declared by Detterman (1994, p.36) ‘a complex human characteristic like intelligence and a complex biological structure like the brain are not going to converge easily’. Hence, it is not unexpected that there is no generally accepted theory which can clarify the source of individual differences in cognitive abilities at the neuronal level. Instead, there is a group of theories which try to link intelligence with specific properties of the human brain (Vernon, 1993). These theories are based on the assumption that some cognitive processes, or even some basic features of the cognitive abilities closely related to intelligence, can also be observed at the brain level.

Several candidates have been suggested as a possible single variable that could explain individual differences in intelligence.

Most common of these is speed of processing as indexed by measures of reaction time and other speeded tests (Vernon, 1987). In most studies, correlations between IQ and measures of speed of processing are around r=.30, which is about average for most cognitive tasks. It is not unexpected that the psychophysiological method mostly utilized in this research is the event-related potential (ERP) technique with its excellent temporal resolution. Latency of the ERP components can be used as the marker of timing of cognitive processes. Findings from studies exploring the problem of the relationship between fluid intelligence and the speed of information processing will be presented in the later section.

Another concept which was supposed to shed light on the biological basis of intelligence was the efficiency of transmission of nervous impulses (A.E. Hendrickson, 1982). Low error rate during information transmission should result in its precise representation at later stages of processing and therefore a more-adjusted behavioral response could be executed. In contrast to this, high error rate can be related to misrecognition of information and behavioral maladjustment.

Other authors also suggest that differences in brain efficiency can be the substratum of differences in fluid intelligence (Haier et al., 1988; 1992). This efficiency can be related to lower energy consumption or engagement of smaller number of neurons. In other words, high intelligence can be associated with a more thrifty brain.

Several significant neural correlates of IQ test scores have been documented, but it is not at all clear that variation in the level of cognitive abilities can be actually caused by variation in these aspects of the nervous system.

## Hendrickson's Transmission Error hypothesis

The advent of the event-related potential (ERP) technique created new possibilities to search for electrophysiological indices of intelligence. The first studies were mainly focused on ERP amplitudes and latencies, but the outcomes were unconvincing and controversial. A new method of analysis was proposed by Rhodes, Dustman and Beck (1969), who reported a significant positive correlation between an index they termed 'the excursion measure' and IQ. This index was actually the contour length of the ERP waveform as traced out by a map-reading wheel. The authors tested twenty 10-11 years old participants using the Wechsler Intelligence Scale for Children (WISC). They have reported positive correlation between 'the excursion measure' and the level of intelligence. A similar method was adopted by D.E. Hendrickson and A.E. Hendrickson

(1980) who reanalyzed the ERP data originally published by Ertl and Schafer (1969) and reported a highly significant positive correlation (r=.77) between WISC scores and an ERP parameter that they called 'the string measure'. This parameter was operationally identical to that proposed by Rhodes, Dustman and Beck (1969), although in all subsequent studies the term 'string length' has been used rather than the original term proposed by Rhodes et al. In two succeeding studies similar findings have been reported. Blinkhorn and D.E. Hendrickson (1982) obtained a positive correlation of 0.84 between 'string length' and performance on Raven's Advanced Progressive Matrices (RAPM, Raven, Court and Raven, 1983) tested on a group of students. Significant positive correlations were also reported by D.E. Hendrickson (1982) between 'string length' and the IQ for a sample of 219 children and 16 adults. These results became the empirical background for the original theoretical attempt to explain the biological basis of fluid intelligence in terms of neural transmission errors (A.E. Hendrickson, 1982).

Hendrickson's hypothesis suggests that the number of errors in signal transmission in the brain is the source of individual differences in intelligence. Higher intelligence can be associated with a lower transmission error rate and vice versa. What is much more interesting, the author proposed that this relationship can be observed in the different complexity of the ERP and can be measured as the 'string length'. Specifically, high error rate obtained during information transmission in the brain should result in a high variability between ERP responses in trials measured up to 250 ms poststimuls, while the low error rate should produce more similar ERP responses in successive trials. Thus, as the result of averaging, high transmission error rate should be connected with low complexity of the average ERP response, while the low error rate can be linked with much more complex waveform. This hypothesis came at a time of renewed interest in the biological basis of cognitive abilities that caused the high popularity of Hendrickson's idea for the next almost twenty years. However, the results of subsequent work varied considerably. Only some of these studies (Haier et al., 1983; Gilbert et al., 1991; Stough et al., 1990) have reported positive correlations between IQ and 'string length'. Other researches have reported correlations near zero (Shagass et al., 1981; Burns et al., 1996; Bates et al., 1995). Significant negative correlations between 'string length' and measures of intelligence were also obtained from some studies (Barrett and Eysenck, 1992; Bates and Eysenck, 1993a). These findings were actually contrary to Hendrickson's hypothesis.

Work in this area has been reviewed by Eysenck and Barrett (1985), Deary and Caryl (1993) and Burns, Nettelbeck and Cooper (1997). The 'string measure' was criticized for being non-specific and consequently not useful in pursuing an understanding of the processes underlying the relationship between structure and function of the human brain and intelligence (Burns, Nettelbeck and Cooper, 1997). Specifically, they found that 'string measure' is dependent on the amplitudes of the ERP as well as the higher frequency

activity within the ERP. Similar objections were raised by Barrett and Eysenck (1994) who reported that removal of the high frequency activity eliminates a part of the event-related activity that was contributing to the correlation between the 'string measure' and IQ. The critique of the Hendrickson model was also provided by Robinson (1993; Robinson and Behahtani, 1997) who insisted that the measure is of little use, either practically or theoretically, as it was sensitive to so many factors. He also pointed out that 'string length' confounds frequency and amplitude differences which might influence the shape of the waveform. He also demonstrated that the Hendrikcson theoretical model is at odds with contemporary knowledge about neural processes.

Some inconsistencies in results reported from studies using the Hendrickson's measure may be explained by the influence of at least two, specific factors. The first factor consistently influencing the relation between 'string length' and the level of intelligence is intensity of stimuli. Significant positive correlations between the complexity of ERP responses and cognitive abilities were obtained from studies where relatively high intensity of auditory or visual stimuli has been utilized (Blinkhorn and D.E. Hendrickson, 1982; Haier et al., 1983; D.E. Hendrickson, 1982). Much weaker relationship has been reported from studies where strength of stimulation was lower (Shagass et al., 1981). This effect was clearly demonstrated by Haier et al (1983). They measured ERP responses to flashes of four different intensities and they found positive correlation between 'string length' and scores on Raven's Advanced Progressive Matrices only for the two highest light luminance levels. At the same they also reported larger associations between IQ and amplitude measures, especially the relative N1-P2 amplitude, than 'the string length' itself and therefore they suggested that 'string length' is rather the by-product of the relative difference of amplitudes of these early components.

The second factor which can modulate the relationship between intelligence and measures of ERP complexity is the engagement of attention. Bates and Eysenck (1993) suggested that when participants passively perceive stimuli used to elicit the ERP response then a positive correlation between 'string length' and IQ can be expected (Blinkhorn and D.E. Hendrickson, 1982; D.E. Hendrickson, 1982; Stough, Nettelbeck and Cooper, 1990; Haier, Robinson, Braden and Williams, 1983). However, when stimuli are hard to ignore or the experimental instruction is unclear, then the correlation could be near zero (Shagass, Roemer, Straunanis and Josiassen, 1981). Moreover, when instruction demands active response to stimuli and attention is engaged in task performance then a negative correlation can be obtained (Barrett and Eysenck, 1992; Bates and Eysenck, 1993; Bates, Stough, Mangan and Pellett, 1995). Therefore, it can be concluded that the relationship between measures of ERP and intelligence is not simple and can be additionally modulated by attention engagement.

## Transmission Speed hypothesis

There is a long-standing hypothesis that higher mental ability, as defined by psychometric tests of intelligence, may be determined, in part, by faster neural transmission time (Ertl and Schafer, 1969). At the present time, this hypothesis still appeals to the well-established fact that individuals scoring higher on IQ tests exhibit faster behavioral response times during the performance of simple sensory, motor, memory and decision tasks than do individuals with lower ability (Jensen, 1982; Vernon, 1990). Therefore, a negative relationship between IQ and temporal characteristic of the ERP can be expected. Additionally, Inspection Time (IT), the minimum exposure duration needed for reliable discrimination of a stimulus, has been widely found to correlate negatively with measures of intelligence (Kranzler and Jensen, 1989; Nettlebeck, 1987; Bates and Eysenck, 1993b). Inspection Time is often assessed in a backward masking task in which the target to be identified is presented briefly and replaced by an overwriting masking stimulus. This methodology was also applied in several studies on the relationship between intelligence and speed of information processing. Another method used in such research is the estimation of the nerve conduction velocity (NCV) by measuring head length or height and dividing this value by the latency of the ERP components (Reed and Jensen, 1992, Reed, Vernon and Johnson, 2004). Similarly, peripheral NCV can be estimated by recording transmission of impulses in median nerve (Vernon and Mori, 1992; Vickett and Vernon, 1994) or in specific reflex arcs (Vernon, 1993). Findings reported in studies utilizing all these methods are briefly presented in the next paragraphs.

According to the hypothesis that higher intelligence can be associated with greater speed of information processing, it is reasonable to expect that information transmission between neurons and structures of the nervous system should be faster in subjects scoring higher in IQ tasks. Vernon and Mori (1992) have reported that there is a highly significant positive correlation between general IQ and NCV from median nerve. Wickett and Vernon (1994) replicated the Vernon and Mori study and reported that intelligence is not related to peripheral NCV in women. They also reanalyzed the Vernon and Mori data and found a significant positive correlation between IQ and peripheral NCV only for men. Similar findings were also reported by Tan (1996). However, other authors did not find a significant relation between these two measures (Barrett et al., 1990). In two different studies (Reed and Jensen, 1992; Reed, Vernon and Johnson, 2004) authors reported that a positive relationship between IQ and NCV can also be observed in the case of the visual tract. Some of these findings suggest that neurons from the brain of highly intelligent subjects are able to transfer information with significantly greater speed

in comparison to low-IQ scorers. However, methodologies of these studies were strongly criticized as being invalid (Saint-Amour et al., 2005).

Moreover, there is no reason to expect that high intelligence is linked with greater neuronal speed only in men, but not in women. Clearly, these peripheral nerves are not directly involved in mental activity that is associated with intelligence. In a recent review of about 10 studies, it was concluded that ''the evidence for an NCV-IQ correlation is weak and mixed'' (Vernon, Wickett, Bazana, and Stelmack, 2000). These NCV-IQ correlations ranged from 0.62 to -0.61 with a mean correlation of 0.18. On the other hand, Reed and Jensen (1992) reported also a negative correlation between general intelligence and the latency of a positive wave at about 100 ms poststimlus. A similar effect was also reported by Burns, Nettlebeck and Cooper (2000) using essentially the same procedures. Therefore, it can be suggested that instead of using very inadequate measure of the NCV, the analysis of latencies of ERP components can be better to test the transmission speed hypothesis.

Latencies of ERP components were used as indices of timing of information processing in the study of Zurron and Diaz (1998). They recorded brainstem (BAEP) and middle-latency (MAEP) auditory evoked potentials and correlated their latencies with the subjects' scores in WISC. Additionally, they used passive and active versions of the oddball task to elicit long-latency ERPs. They did not find any relationship between intelligence and latencies of BAEP or MAEP components. The only significant negative correlation found in this study was between IQ and P3 latency. Consistent with this, results from another study (Stelmack, Knott and Beauchamp, 2003) using BAEP recording did not support the transmission speed hypothesis either. The authors reported that higher IQ was associated with longer latencies of BAEP, which contradicts this hypothesis. From previous reviews of this work (Deary and Caryl, 1993; Stelmack and Houlihan, 1995), it can be concluded that there is no reliable relation between mental ability and the latency of early, exogenous ERP components recorded in response to simple repetitive sensory stimulation.

In several studies that examined the relation of mental ability and speed of sensory discrimination using an ERP recording procedure, the backward-masking paradigm was used. Most of the research was conducted in the visual modality using the Inspection Time (IT) task. In general, these studies exhibited varying degrees of success (Stelmack and Beauchamp, 2001). Some authors have reported that measures of intelligence can be related to differences in the rising phase of the P2 component of the ERP elicited by IT stimuli (Caryl, 1994; Caryl, Golding and Hall, 1995; Morris and Alcorn, 1995; Zhang, Caryl and Deary, 1989). These findings were interpreted as evidence that high intelligence is connected with greater speed of information transfer from the sensory register to short term memory. What should be noticed, however, is that no significant

differences in the latencies of early ERP components between groups differing on IQ score have been found. The only exception is the study by Burns et al. (2000) which reported negative relationships between the level of cognitive abilities and the latencies of P1, N1 and P2 components elicited by IT stimulus. In this study EEG activity was recorded concurrently with the presentation of the target stimuli and then an ERP waveform was derived by averaging across a range of interstimulus intervals that may vary between individuals (high IQ subjects were presented with short IT stimuli duration, low IQ receive longer presented IT stimuli). Such analysis seems to confound the effect of IQ differences with the effect of differences in stimulus duration. Thus, it is possible that the effects observed in this study can be related to processes involved in analysis of visual stimuli (stimulus duration) rather than the individual differences (intelligence). Therefore, it is not clear how the individual differences in fluid intelligence are related to the speed of processing as it is revealed by early ERP components.

In contrast to this, there is a growing body of evidence that a high level of IQ can be associated with shorter latency of the P3 (or P300) component. This component is consistently related to attention, decision making and memory updating (see Polich and Criado, 2006; Polich, 2007 for review). Latency of the P3 is considered to be closely related to voluntary stimulus evaluation time (Kutas, McCarthy and Donchin, 1977). Several studies reported shorter P3 latency for subjects scoring high in an IQ test in comparison to those with lower IQ score. This effect has been observed in experiments where the traditional oddball paradigm was used to elicit the P3 response (Ladish and Polich, 1989; O'Donnell, Friedman, Swearer and Drachman, 1992; Polich, Ehlers, Otis, Mandell and Bloom, 1986; Polich, Howard and Starr, 1985; Polich and Martin, 1992; Walhovd and Fjell, 2002; Zurron and Diaz, 1998). Shorter P3 latency was also associated with higher fluid intelligence in studies that employed an auditory discrimination task with backward masking, a modification of the oddball paradigm (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Sculthorpe, Stelmack and Campbell, 2009; Troche et al., 2009). Additionally, there is also evidence that the amplitude of P3 can be related to intelligence. However, the relation between cognitive ability and P3 amplitude is not as clear. Positive correlations between measures of intelligence and P3 amplitude are consistently reported from oddball studies (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; De Pascalis et al., 2008; Fjell and Walhovd, 2003; Jaušovec and Jaušovec, 2000; Sculthorpe, Stelmack and Campbell, 2009; Troche et al., 2009). Similar effects were also obtained using the IT paradigm (Alcorn and Morris, 1996). However, there is a group of studies reporting negative correlations (Houlihan, Stelmack and Campbell, 1998; Zhang, Caryl and Deary, 1989) or no reliable relationship between intelligence and P3 amplitude (Polich and Martin, 1992). Taken together, these findings suggest that intelligence influences the patterns of brain activity

at a relatively late stage of information processing. It should be remembered that the P3 component can be linked with attentional resource allocation and its latency is proportional to stimulus evaluation timing. Therefore, the shorter latency and higher amplitude of the P3 component observed in participants scoring higher in IQ tests can be related to a greater speed of classification of relevant information and more intense attentional resource allocation. Due to this, it can be expected that brain areas specifically involved in attention and stimulus classification should be differently activated in subjects differently performing in intelligence tests.

## Neuroimaging studies

Recently several functional studies were conducted to explore the neural basis of fluid intelligence. Generally, three different approaches have been used by researchers to identify the brain correlates of individual differences in cognitive abilities. While some of the studies were aimed at identification of specific differences in brain functioning between subjects differently scoring on IQ tasks (Haier et al., 1988; Haier et al., 1992; Larson et al., 1995; Gray, Chabris and Braver, 2003; Lee et al., 2006), others were focused on recognition of brain structures closely linked with the processes involved in fluid reasoning itself (Prabhakaran et al., 1997; Duncan et al., 2000). The goal of a third group of studies was to discover intelligence-related differences in brain anatomy (Haier et al., 2004; Haier et al., 2010). These studies differ in the methods of brain imaging (fMRI and PET) as well as the methods of statistical analysis which were adopted. Therefore, it should be noted that they sometimes cannot be directly compared.

One of the earliest neuroimaging experiment aimed at brain correlates of individual differences in fluid intelligence was conducted by Haier and his colleagues (Haier et al., 1988) using positron emission tomography (PET). In this experiment, a small group of young healthy men (n=8) did an abstract reasoning test (Raven's Advanced Progressive Matrices RAPM) after the injection of $^{18}$fluoro-2-deoxyglucose (FDG), which has an uptake time of 30 minutes. The brain activity was measured at three selected slices. Each of the slices was divided into 8 sectors and then analyzed using two different approaches. The Glucose Metabolic Rate absolute index (GMR) was defined as the absolute metabolic rate within each sector, while the GMR relative index was computed as the sector metabolic rate divided by mean-glucose metabolic rate in the whole slice. Results obtained from this experiment suggest that the RAMP scores correlated negatively with the absolute indexes of GMR. Correlation between the scores on the intelligence task and relative indices were found to be not significant. These findings were interpreted as proof that in normal young adults for whom a cognitive task is relatively

difficult (low RAPM scorers), more cortical activity is necessary to perform the task. The authors also suggest that poor performing normal subjects have less efficient neural circuitry when compared to high RAPM scorers. This inefficiency can be related to higher energy consumption by each neuron or the use of more neurons to perform the task. The differentially efficient brain regions were located in sectors corresponding to the parietal cortex and, to a lesser extent, the frontal cortex. These results were confirmed by the second study reported by the same group (Haier et al., 1992). In this experiment a similar method of measurement of brain activity was implemented (injection of $^{18}$fluoro-2-deoxyglucose). The experimental procedure was, however, different. Two different intelligence tasks were completed by 8 subjects (Raven's Advanced Progressive Matrices RAPM and the Wechsler Adult Intelligence Scale-Revised WAIS-R). Two PET scan sessions were separated by a learning period (4-8 weeks). During each uptake phases subjects played the Tetris game, which they had to learn during the learning period. Brain activity observed for the 'naïve' and 'practiced' session was then correlated with the scores from IQ tasks. A significant positive correlation between RAPM scores and the whole-brain GMR was obtained for the 'naïve' session ($r=.77$ $p<.05$), while for the 'practiced' session, no significant correlation was observed. At the same time, a significant negative correlation between the RAPM score and the between session change in GMR was found ($r= -.68$ $p<.05$). Here, significant negative correlations were found for the superior frontal gyrus, the anterior cingulate gyrus, the posterior cingulate gyrus and the paracentral lobule. The authors concluded that results from this study are consistent with their efficiency hypothesis. Specifically, the subjects with higher IQ, which showed larger GMR decrease between sessions, manifest also a higher level of automatic processing after training. This resulted in fewer extraneous brain areas being used for the task. What should be noted, the authors ignored the fact that positive correlation obtained for 'naïve' session is clearly inconsistent with this hypothesis.

The results from these two experiments provide the background for the efficiency hypothesis linking high fluid intelligence with the more economically functioning brain. According to this, lower brain activity for the more intelligent person can be expected. This hypothesis became very popular at the end of the last century. However, many later conducted neuroimaging studies brought results which are at odds with this hypothesis.

Larson and his coworkers (1995) contrasted PET data gathered on participants who solved two working memory tasks differing in difficulty. These tasks were tailored to the participants' own ability levels. Subjects were also pretested on RAPM to select high- and average-RAPM groups. Obtained results suggest that the more demanding the task, the higher is the FDG metabolic rate. What is even more interesting in the context of this thesis, is that high-RAPM scorers tended to exhibit higher cortical metabolic rates than participants in the lower IQ group. The obtained effect was most evident for frontal and

parietal regions. This finding implies that high cognitive efficiency is not invariably linked with low cortical metabolic rate, as was suggested by Haier et al. (1988). Even more suggestive results were obtained by Gray, Chabris and Braver (2003) who utilized an event-related fMRI technique to test whether general fluid intelligence can be mediated by brain regions that support attentional control. Participants performed two challenging 3-back tasks inside the scanner. The authors reported that RAPM scores correlated positively with the magnitude of event-related activity in the lateral prefrontal cortex (PFC), the dorsal anterior cingulate, and the cerebellum. Similar relations were observed within parietal and temporal cortex as well. They also performed multiple regression analysis, and found that neural activity within the left PFC and the parietal cortex (bilaterally) simultaneously explained more that 99.9 % of the relationship between general fluid intelligence and accuracy measured in the most demanding trials. A positive relation between the level of cognitive abilities and indexes of brain activity was also reported by Lee at al. (2006). They found that brain activity observed for a more demanding task (high g-load) was higher than a less difficult task (low-g load). At the same time, the between task difference in parietal activity was found to be positively correlated with measures of intelligence.

Results from these studies testing the relation between fluid intelligence and the level of brain activity are mixed. Findings reported by Haier and his group (1998, 1992) suggest that a high level of mental abilities can be linked with less brain activity, possibly representing grater neural efficiency. In contrast to this, results obtained by others (Larson et al., 1995; Gray, Chabris and Braver, 2003; Lee et al., 2006) indicate that high fluid intelligence is associated with greater brain activity. At the same time, activity from similar brain regions is reported to be connected with differences in intelligence in all these studies. The lateral frontal cortex and the parietal cortex are two main candidates as the neural substrates of fluid intelligence. Two other brain regions (the anterior cingulate gyrus and cerebellum) were reported only by Gray et al. (2003).

A similar group of brain structures was also suggested by findings obtained from neuroimaging studies specifically focused on exploring the functional anatomy of intelligence. In all these studies two or more distinctly g-loaded tasks were contrasted to reveal brain areas exclusively linked with fluid reasoning. Such an approach was adopted by Prabhakaran et al. (1997), who compared fMRI activity recorded in three different tasks. They found greater activity for an analytic task localized in the prefrontal, cingulate, parietal and occipital regions when compared to a low g-loaded matched task. A similar pattern was also observed when brain activity measured in the analytic task was contrasted with a figural task. These findings suggest that the prefrontal cortex, together with the superior parietal region, is crucial for fluid reasoning. Consistently, an analogous conclusion was drawn by Duncan et al. (2000), who measured PET responses in two

differently g-loaded tasks. They reported that higher brain activity in the task was highly correlated with standard measures of fluid intelligence when compared to a task with lower g-load. The brain regions where the significant effects were observed were located in the lateral and medial frontal cortex, the parietal lobe, and occipital cortex. These effects were also confirmed by Lee et al. (2006). Using fMRI, they found greater bilateral activity in the lateral prefrontal and medial frontal areas when a complex high g-loaded task was contrasted with a much simpler one. A similar pattern of results was also obtained in this study for the parietal and occipital cortex. Results obtained in these three experiments indicate the importance of the prefrontal cortex, along with posterior cortical regions, in solving tests that might generally be classified as reflecting fluid intelligence. These findings are also consistent with reports from studies where anatomical distinctions between subjects differing in intelligence were tested (Haier et al., 2004, 2010; Li et al., 2009).

## Aim of thesis

The main aim of the experiments presented in this thesis was to investigate the relationship between fluid intelligence and the functioning of the neuronal correlates of the attention system. To achieve this, brain activity was recorded using event-related potentials (ERPs) methodology, in subjects distinguished by their score on psychometric tests of intelligence. Specifically, latency and amplitude of the P3 component of the ERP were used as indices of the early phase of attentional resource allocation. These indices were then correlated with the scores of IQ tests obtained from participants in order to test whether differences in fluid intelligence can be related to specific brain correlates of attention. Such supposition was based on findings from previous studies in this field. On the basis of the results obtained from those studies, several preliminary conclusions can be drawn which provide the context for the studies provided here.

Firstly, attention can influence the relation between the measures of brain activity and the measures of cognitive abilities. Despite the fact that measures of ERP complexity have been criticized extensively for being non-specific and theoretically irrelevant (Burns, Netttlebeck and Cooper, 1997; Robinson, 1993; Robinson and Behbehani, 1997), results from experiments suggest that the relationship between brain responses and measures of fluid reasoning depends on the conditions in which electrophysiological activity is measured. This has been previously postulated by Bates and Eysenck (1993) who found that the direction and the strength of relationship between indexes of ERP complexity and scores on IQ tests depend on the magnitude of attention engagement in task performance. Thus, it can be suggested that a much more reliable link between measures

of cognitive performance and brain activity can be established when subjects are tested in conditions demanding at least some engagement of cognitive processing in the experimental task.

Secondly, it was found recently that when attention is engaged in task performance the speed of information processing can be related to the level of fluid intelligence. Specifically, a shorter latency time of the P3 component for subjects scoring high on IQ tests has been reported consistently (Bazana & Stelmack 2002; Beauchamp & Stelmack 2006; DePascalis, Varriale & Matteoli 2008; Sculthorpe, Stelmack & Campbell 2009; Troche et al 2009; Zurron & Diaz 1998). It was also found that P3 latency increases with normal aging (Polich, 1996; Fjell and Walhovd, 2001), and peak timing increases as mental capability is compromised by dementia (O'Donnell et al., 1992; Polich et al., 1986, 1990; Polich and Corey-Bloom, 2005; Potter and Barrett, 1999). At the same time, no such strong evidence has been found for earlier ERP components. What should be also noted, is that the major interpretation of the P3 component is that it indexes cognitive processes related to attentional resource allocation and stimulus evaluation (Kok, 2001; Polich and Criado, 2006; Polich 2007). Therefore, latency of the P3 can be considered to be a measure of *stimulus classification* speed, rather than *response selection* processes (Kutas, McCarthy and Donchin, 1977; McCarthy and Donchin, 1981).

Also important in this context, is that P3 represents the summation of activity from various widely distributed areas in the brain, and cannot be considered as a unitary brain potential. Moreover, a distinction can be made between several subcomponents which temporally overlap (Polich and Criado, 2006). It is generally accepted that at least two major subcomponents can be differentiated, namely the P3a and the classical P3 (or P3b). A growing body of evidence suggest that these two components differ in their scalp distribution, magnitude, and peak latency as a function of the stimulus meaning. Therefore, it can be suggested that the P3a and P3b reflect distinct, although strongly linked, information processing events. Early P3a, peaking maximally at fronto-central locations, can be associated with the initial attention reallocation resulting from detection of the stimulus attribute change. This process follows the initial sensory processing and stimulus feature mismatch detection. In contrast, the later P3b, with its parietal maximum, can be related to voluntary stimulus classification. This process should engage a working memory comparison, while the neuronal model of the stimulation is compared with the attentional trace of relevant information. It is reasonable to assume that the stimulus deviance detection initially engages attention (P3a) to facilitate the stimulus meaning assessment (P3b) associated with memory operations.

Taken together, speed of information processing, indexed by the latency of P3 complex, seems to be inversely related to the level of intelligence. On the other hand, it is still not clear to what extent a similar relationship can be observed when the distinction

between P3a and P3b components is made. Moreover, there is evidence that amplitude of P3 can be linked with differences in IQ. However, the relationship between P3 amplitude and intelligence is far from clear.

Thirdly, intelligence-related differences in hemodynamic responses reported in previous studies were localized mainly in the dorsolateral prefrontal cortex, the anterior part of the cingulate gyrus, and in the superior parietal cortex (Duncan et al., 2000; Gray, Chabris and Braver, 2003; Larson et al., 1995; Lee et al., 2006; Prabhakaran et al., 1997). All these brain regions are commonly related to the attention system of the brain (Mesulam, 1981; Posner and Petersen, 1990; Webster and Ungerleider, 2000). It should also be noted, that there is growing evidence that the dorsolateral prefrontal cortex is the source of the P3a component. At the same time, the superior parietal cortex is suggested as the part of the neural network involved in P3b generation (Polich and Criado, 2006; Polich, 2007).

## Summary of experiments

The primary objective of this thesis was to study the relationship between the level of fluid intelligence and attentional resource allocation. This was done by measuring P3 component of event-related potentials (ERP) elicited by auditory and visual stimuli in different experimental conditions. Specific aims of the experiments were to investigate the relation between attentional functioning and characteristics of the P3a and P3b components, to define their cortical generators, and to specify the connection between differences in ERP parameters and measures of fluid reasoning. Amplitudes and latencies of P3 were therefore compared between groups scoring differently on IQ tests. The Raven's Advanced Progressive Matrices test (RAPM) was used to measure the level of fluid intelligence. The RAPM is a widely used nonverbal test designed to be a culture-free measure of fluid reasoning that does not rely on crystallized knowledge. Therefore, it is thought to provide an optimal measure of processes widely used in fluid reasoning. This property of Progressive Matrices was previously demonstrated by Snow, Kyllonen, and Marshalek (1984) using a multidimensional scaling analysis. They found that the Raven's test occupied a central position among all the tests measuring cognitive abilities. This indicates that it provides the optimal domain-independent measure of fluid reasoning processes relevant for many kinds of problem solving. On the other hand, amplitude and latency of P3 subcomponent provides information about timing and intensity of neural processes closely related to attention mechanism. Specifically, early P3a can be linked with initial attention reallocation while later P3b is associated with voluntary stimulus classification. Hence, establishing the relation between measures of fluid reasoning and

activity of attention mechanism reflected in basic characteristic of P3 will be important step toward the model of neural basis of intelligence.

In the first experiment, described in Chapter 2, basic characteristic of frontal and parietal P3 subcomponents were investigated. The specific question in this experiment was how the basic features of auditory P3 subcomponents would be affected by the simultaneous presentation of irrelevant visual stimuli, which were expected to involuntarily engage attention. In the following experiment, presented in Chapter 3, the essential attributes of P3 subcomponents were further investigated using passive and active versions of the auditory three-stimulus oddball paradigm. The experimental design allowed a direct comparison of timing, and the scalp distributions, of P3a and P3b elicited in two conditions differently engaging the attention system. It enabled us to specify whether these two subcomponents, measured in different conditions, reflect similar physiological processes. The aim of the third experiment, described in Chapter 4, was to define the scalp topography of the two subcomponents of the P3 elicited in a three-stimulus oddball paradigm, and to identify their cortical generators, using the source localization method. In the fourth experiment (Chapter 5) the relation between timing and magnitude of auditory P3 subcomponents, and measures of fluid intelligence, was directly tested. The purpose of this study is to determine the pattern of intelligence-related differences in activity of attention mechanism as it can be reflected in basic characteristic of auditory P3a and P3b. Additionally, neuronal sources of the effect were specified. In the fifth experiment (Chapter 6) intelligence-related differences in P3 amplitude were tested using visual stimuli. The aim of this experiment was to establish whether the differences in basic characteristic of P3 responses elicited by visual stimulation are similar to that observed when auditory stimuli were used.

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# CHAPTER 2

## THE P3 PRODUCED BY AUDITORY STIMULI PRESENTED IN A PASSIVE AND ACTIVE CONDITION: MODULATION BY VISUAL STIMULI *

**Abstract**

The aim of this study was to investigate how the processing of auditory stimuli is affected by the simultaneous presentation of visual stimuli. This was approached in an active and passive condition, in which a P3 was elicited in the human EEG by single auditory stimuli. Subjects were presented to tones, either alone or accompanied by the simultaneous exposition of pictures. Two different sessions were applied. In the first session the tones demanded no further cognitive activity from the subjects (passive or 'ignore' session), while in the second session subjects got the instruction to count the tones (active or 'count' session). The central question was whether inter-modal influences of visual stimulation in the active condition will modulate the auditory P3, in the same way as in the passive condition. Brain responses in the ignore session revealed only a small P3-like component over the parietal and frontal cortex, however, when the auditory stimuli co-occurred with the visual stimuli, an increased frontal activity in the window of 300-500 ms was observed. This could be interpreted as the reflection of a more intensive involuntary attention shift, provoked by the earlier visual stimulation. Moreover, it was found that cognitive load, caused by the count instruction, resulted in an evident P3, with maximal amplitude over parietal locations. This effect was smaller when auditory stimuli were presented on the visual background. These findings might support the thesis that available resources were assigned to the analysis of visual stimulus, and, thus, were not available to analyse the subsequent auditory stimuli. This reduction in allocation of resources for attention was restricted to the active condition only, when the matching of a template with incoming information results in a distinct P3 component. It is discussed whether the putative source of this effect is a change in the activity of the frontal cortex.

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## Introduction

There is common agreement that attention is a complex phenomenon influencing perceptual processing and enabling perceptual awareness of attended events. There is also general consensus that attention could be divided into at least two different forms. Involuntary attention, also described as exogenous or orienting attention, is closely related to changes in brain processes evoked by occurrence of unexpected event in the surroundings. This kind of changes lead to attention switch and are the bottom-up processes in nature. On the other hand, attention is also related to voluntary detection of relevant objects which characteristic was previously loaded to working memory. This type of attention, sometimes called endogenous or executive, utilizes process of top-down modulation and is much more closely related to conscious processing and controlled reacting. Voluntary form of attention is also closely linked with selective function of attention (Posner, 1995).

Event-related potentials (ERP) provide a valuable index of covert sensory and cognitive processing in humans. Probably no other ERP component is considered to be closer related to attention than the P3. The P3 component of the ERP, with a peak latency of 300-500 ms is commonly obtained in an oddball paradigm (Picton, 1992), but P3 responses with a similar topography can also be generated in a single stimulus task (Mertens and Polich, 1997; Strüber and Polich, 2002). There is general agreement that P3 is not a unitary brain potential but represents the summation of activity from various widely distributed areas in the brain and distinction can be made between two subcomponents, which temporally overlap, namely the P3a and the P3b (Hruby and Marsalek, 2003). The P3a is a large, positive deflection with a frontocentral distribution that is elicited by novel and non-target stimuli and that mainly reflects an alerting process in the frontal lobe while involuntary attention shifts to changes in the environment takes place (Yamaguchi and Knight, 1991a). P3a is easily obtainable in response to auditory or visual deviant non-target events in an oddball paradigm (Katayama and Polich, 1998; 1999). In contrast, the P3b has a more posterior-parietal scalp distribution and somewhat longer latency than P3a. There is broad evidence that P3b could be regarded as reflecting target stimulus classification or evaluation in tasks that require some form of action like a covert or overt response to meaningful stimuli, when voluntary attention is engaged (Donchin and Coles, 1988; Kok, 2001; Polich, 1998). The distinction in P3a and P3b is evident for both auditory and visual modalities, although the P3 elicited by auditory stimuli differs from the P3 evoked by visual stimuli in some qualities. For example, the amplitude of the visual P3 is higher than the auditory P3 (Gonsalvez and Polich, 2002; Katayama and Polich, 1999).

The relationship between involuntary and voluntary attention, as indexed by P3a and P3b subcomponents, could be studied in both auditory and visual modalities. For example, Katayama and Polich (1999) found that amplitude of auditory P3a is determined by the strength of attentional focus. The more difficult discrimination between targets and standards was the bigger the P3a response to rare non-targets. These results demonstrate that voluntary attention could modulate the involuntary response to irrelevant but unexpected events. Similar effect was also reported for visual modality (Comerchero and Polich, 1999). However, it is not clear if the observed effects are modality specific, despite its similarities, or if it reflects engagement of supramodal attention mechanisms. Results from crossmodal spatial attention studies suggest that directing attention in relevant modality to one space location modulate early modality-specific ERP components not only for that modality, but also for currently irrelevant modalities. For example, the initial modality specific components of the visual ERP are typically larger for stimuli at voluntarily attended locations than for stimuli at unattended locations (Luck and Girelli, 2000). Similarly, auditory stimuli that appear at voluntarily attended locations evoke a larger negativity in the 60-200 ms range over the fronto-central locations than sounds that appear at unattended locations (Näätänen, 1990; Teder et al., 1993). These effects are commonly interpreted as the evidence of attention based facilitation of perceptual processing. Similar effect of attention could also be observed across modalities. It was found that selective attention across modalities also influences early stages of sensory processing. Specifically, auditory stimuli that appear at voluntarily attended locations evoke enlarged early negativities (100-200 ms) even when viewers respond only to visual stimuli that appear at the attended location and ignore auditory stimuli irrespective of its origin in space (Eimer and Schröger, 1998; Eimer et al., 2004; Hillyard et al., 1984; Teder-Sälejärvi et al., 1999). Similar crossmodal effects take place for visual stimuli when viewer voluntarily attends to sounds at a particular location (Eimer and Schröger, 1998; Eimer et al., 2004; Teder-Sälejärvi et al., 1999). These results could suggest that the brain mechanisms that mediate spatial shifts of attention to auditory, visual, and tactile stimuli may be supramodal or at least tightly linked.

The open question is however if crossmodal influence could be observed when stimuli in different modalities are not separated in space. Moreover, the question could be raised if the crossmodal interaction could be visible not only at the initial stage of stimulus sensory encoding, but also at the later stage, when voluntarily attention is involved in conscious classification of the stimulation. The issue touched in the present paper is the nature of the interaction between two stimulus modalities: the visual and the auditory modality.

Similar issue was previously approached by Schupp et al. (1997). They showed that the amplitude of P3 response to white noise presented in parallel with visual stimuli

depends on the picture content. They suggested that pictures evoking an emotional response, demanded more attentional resources in comparison to emotionally irrelevant pictures. They found that the more resources the visual stimuli consumed, the greater the reduction of the P3 amplitude evoked by simultaneously presented auditory stimuli was. Cuthbert et al. (1998) also found a smaller P3 elicited by auditory stimuli when simultaneously affective visual stimuli were presented when compared to P3 obtained in response to the same sounds but exposed concurrently with neutral picture. This effect was comparable under attended and unattended conditions. Oray et al. (2002) reported a reduced auditory P3 amplitude when recorded in response to tone bursts paired with a visual stimulus. They suggested that involuntary attention to visual stimuli might suppress late cognitive processing of auditory events. These results are also consistent with findings that processing of irrelevant visual probe stimuli is suppressed when its exposition takes place shortly after presentation of visual target stimuli in oddball task, but not when the probe was preceded by frequent standard stimulus (Michalski, 2001; Milner and Michalski, 2003).

In all studies the visual and auditory stimuli were presented with a close temporal proximity and only high intensity noise-bursts were tested (Oray et al., 2002). Furthermore, the P3 was evoked only with two different forms of parallel visual stimulation (Schupp et al., 1997; Cuthbert et al., 1998). Hence, so far it is not completely clear whether simultaneous exposure to innocuous visual stimuli influences the processing of auditory stimuli. Also the question whether P3 amplitude is determined by the degree of inter-modal influence, cannot be answered unequivocally. Moreover, another unsolved question is whether in a passive condition, when only a small P3 is expected, a suppression of resources is likely. Thus, the aim of the present study is to examine the effects of a parallel presentation of innocuous, task-irrelevant, visual stimuli on an auditory ERP response. In order to clear up these questions, auditory stimuli are presented alone or accompanied with visual stimuli. To maximize the probability of inducing two distinct forms of cognitive activity, the experiment is divided into two sessions. In the first session, the subjects are instructed to passively perceive auditory events while simultaneously watching visual material or not, whereas in the second session participants are instructed to, silently, count the tones, in order to pay specific attention to the auditory stimuli, again watching visual stimuli or not.

It was predicted that ERP responses, obtained in the two sessions, would differ in the amplitude of the auditory P3. In the active (count) condition, a positive component with a latency of 300-500 ms was expected, but not in the passive (ignore) condition. Moreover, the active condition was designed to facilitate attentional resource allocations and, subsequently, to engage working memory. The positive component, expected in the active condition alone, was thought to a have maximum over parietal locations.

Moreover, tones presented simultaneously with visual stimuli in the active condition, were thought to elicit a reduced parietal P3 component. This expectation was based on the view that attentional demands necessary for the processing of visual stimuli, should result in a reduction of the available resources for the auditory modality, and might effectively weaken processing of this auditory information. However, in the passive condition only a small P3 was expected, implying that a main effect of the visual stimuli on the processing of the tones was not predicted, especially not on the parietal location.

## Methods

### Subjects

Forty two healthy male and female students, with an age range of 19 – 25 years (M=21,7; SD=1,57) took part in the experiment. Participants, reporting no medical or psychological problems, were right-handed and had normal, or corrected to normal, vision, as well as normal hearing. All of them received course points for their participation and signed an informed consent. Due to excessive eye or muscle artefacts ten subjects had to be excluded, thus the final group consisted of thirty two subjects (22 females and 10 males).

### Recording conditions

The EEG was recorded from 3 mono-polar locations (Fz, Cz, Pz) according to the 10-20 international electrode placement system. All the electrodes were placed on the scalp using an electro-cap and were referred to the left mastoid recording. The electrode placed on the forehead served as a ground electrode. Electrode impedance was always less than 5 kOhms. The horizontal and vertical EOG were monitored by 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. The electrical signals were sampled at a rate of 256 Hz with a time constant 10 s (equivalent of high pass filter 0.016 Hz), low pass filtered 30 Hz, and amplified 10 000. Output data were subsequently transferred to and stored in a computer for analysis. The EEG was off-line sampled for 0.7 sec trial (100 ms prior to stimulus onset and 600 ms after stimulus onset). Trials with EOG or EEG activity exceeding 50 micro-volts were rejected and remaining data were corrected for eye-movement artefacts using BrainVision software (Gratton, Coles and Donchin, 1983). The P3 component was defined as the positive-going peak with the highest amplitude occurring within 300-500 ms after onset of stimulus presentation. Peak amplitude was calculated relative to the pre-stimulus baseline, and peak latency was measured from the time of stimulus onset.

**Procedure**

The entire experiments lasted about one hour, interrupted by a short break. Subjects were seated in a darkened sound-isolated, air-conditioned chamber. They were asked to relax and to restrict body movements and blinking as much as possible. Two separate sessions in the experiment were employed. In the first session the subjects were asked to passively perceive the tones and were informed that there was no task associated with the stimuli ('ignore' session), while in the second session the subjects were asked to silently count the tones and report the total number at the end of the session ('count' session). The sequence of stimuli presented was pseudo-random, and was identical for each participant and for each session. This sequence consisted of 45 tones presented without visual stimulation (A condition) and 45 tones presented together with visual stimuli (VA condition). Tones had a frequency of 1 kHz and a duration of 100 ms with 10 ms rise/fall time (62 dB) and were presented through loudspeakers, located behind the chair of the subject. Visual stimuli were back-projected on a screen, located two meters from the subject. Visual stimuli consisted of slides with black neutral geometric figures on a grey background. When tones were presented during the exposition of a visual stimulus, then the interval between slide onset and tone onset varied between 3.5 and 5 seconds. Each slide was presented for six seconds. Inter-trial interval (ITI) varied from 1 to 2 seconds.

**Data Analyses**

Repeated-measures analyses of variance (ANOVA) were performed examining the effect of within-subjects factors of electrode LOCATION along the saggital plane (Fz, Cz, Pz), stimuli presentation CONDITION (auditory vs. visual+auditory; A vs. VA), and SESSION (ignore vs. count) on P3 amplitude and latency. The effects of location were examined in orthogonal three-level repeated-measures location factor, while a Greenhouse-Geiser correction was applied when appropriate. Only the corrected values of P are reported here.

## Results

**Amplitudes of auditory P3**

Figure 1 shows the grand average ERP elicited by tones presented alone and presented on the visual background in both the ignore and count sessions. The P3 component measured during ignore session was clearly visible only on frontal site, while in other cases it was less evident. In case of count session apparent P3 deflections were observed for each location and their amplitudes were significantly bigger in comparison to P3

amplitude obtained in ignore session (main effect of SESSION factor: $F(1,31)=72.75$ $P<0.0001$).

The analysis performed for the count session showed that P3 has a typical topography with its maximum over parietal locations ($F(2,62)=76.63$ $P<.0001$ $\varepsilon=.933$), as indicated in Figure 2. The parietal maximum for P3 was also evident when the analysis was separately done for the tones alone ($F(2,62)= 70.76$ $P<.0001$ $\varepsilon=.962$) as well as for tones occurring on the visual background ($F(2,62)=44.94$ $P<.0001$ $\varepsilon=.935$). On the other hand, when the P3 amplitude in the ignore session was inspected, significant effect of LOCATION was also found ($F(2,62)=23.74$ $P<.0001$ $\varepsilon=.934$). Progressive increase of P3 amplitude was observed when auditory and visual-auditory conditions in ignore session were separately examined ($F(2,62)=32.37$ $P<.0001$ $\varepsilon=.802$ and $F(2,62)=5.78$ $P=.014$ $\varepsilon=.651$, respectively). This suggests that the amplitude of the P3 component obtained in both conditions and in both sessions increased from frontal to parietal locations. However, this change was more steep for P3 measured in count session than for its ignore counterpart what resulted in significant interaction of SESSION × LOCATION factors ($F(2,62)=32.16$ $P<.0001$ $\varepsilon=.984$). Similarly, significant interactions between these factors were also observed when examination was limited to auditory or visual-auditory conditions ($F(2,62)=28.46$ $P<.0001$ $\varepsilon=.912$ and $F(2,62)=10.13$ $P<.001$ $\varepsilon=.796$, respectively).

On the other hand, significantly more abrupt increase of P3 amplitude along saggital plane was observed for auditory condition in comparison to equivalent change obtained for visual+auditory condition (interaction CONDITION × LOCATION: $F(2,62)=9.09$ $P<.001$ $\varepsilon=.845$). Also the significant main effect of CONDITION was found in case of analysis performed across sessions ($F(1,31)=5.19$ $P=.030$). This suggests that auditory P3 amplitude was effectively modulated not only by experimental instruction to count the tones but also by additional visual stimulation. However, when analysis of the effect of CONDITION was separately done for each session, significant result was found but only for the ignore ($F(1,31)=18.84$ $P<.001$), but not for the count session ($F(1,31)=0.04$ $P>.05$). At the same time significant CONDITION × LOCATION interactions were demonstrated in separate analysis for both ignore and count sessions ($F(2,62)=3.73$ $P=.039$ $\varepsilon=.810$ and $F(2,62)=8.95$ $P<.001$ $\varepsilon=.863$, respectively). These results suggest that additional visual stimulation differently modulate amplitude of P3 component obtained in passive and active sessions. This suggestion was partially confirmed by significant interaction CONDITION × SESSION when analysis was performed across all location site ($F(1,31)=8.55$ $P=.006$). However, examination of the effect of interaction CONDITION × SESSION × LOCATION brought no significant result ($F(2,62)=1.43$ $P>.05$ $\varepsilon=.775$).

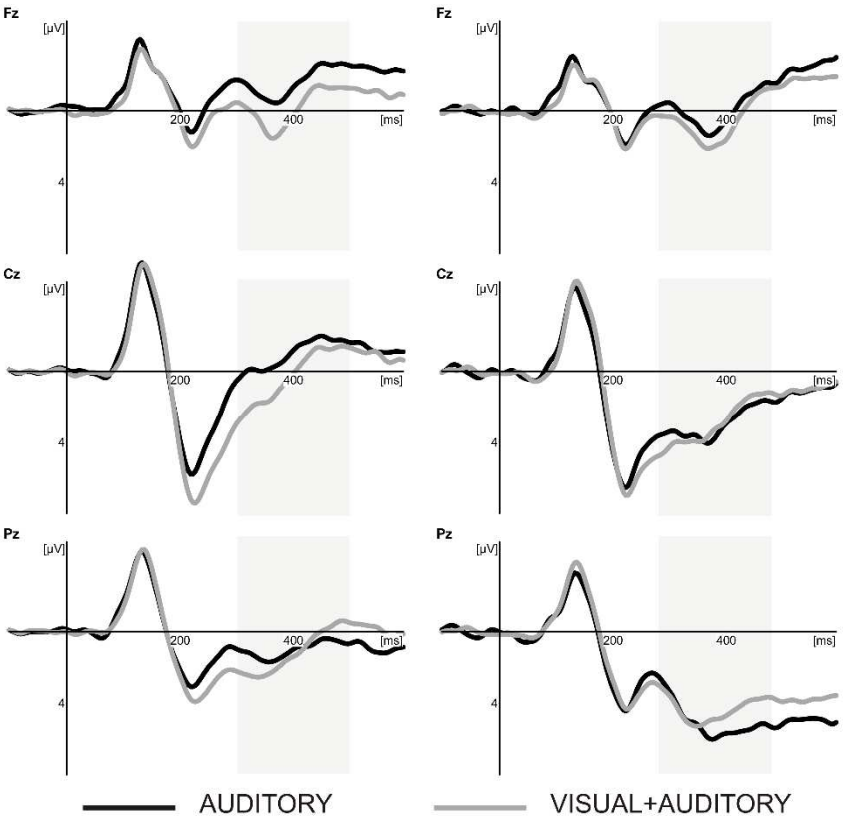


Figure 1. Grand average auditory ERP recorded in ignore (left panel) and count (right panel) sessions. Black lines indicate responses in auditory condition and grey lines represent responses in visual+auditory condition. The latency window of the P3 component (300-500 ms poststimulus) is highlighted.

When effects of experimental instruction and additional visual stimulation were analyzed for frontal location, significant main effects of SESSION ($F(1,31)=21.25$ $P<.0001$) as well as of CONDITION ($F(1,31)=20.80$ $P<.0001$) were found. P3 amplitude obtained in ignore session was lower than amplitude of this component measured in count session. Simultaneously, bigger P3 was observed in response to tones accompanied with visual stimulation in comparison to pure tones. Inspection of CONDITION × SESSION interaction brought almost significant result ($F(1,31)=3.52$ $P=.070$). These result let us suggest that change in task demands as well as additional stimulation in different modality were capable to boost frontal response. When similar analysis was performed for parietal P3, much bigger P3 response to tones was observed for count session in comparison to ignore

session. This was confirmed by highly significant main effect of SESSION (F(1,31)=91.02 P<.0001) was obtained. At the same time, amplitude of P3 component measured in auditory and auditory+visual conditions were not significantly different (main effect of CONDITION: F(1,31)=0.13 P>.05). Inspection of CONDITION × SESSION interaction brought significant result (F(1,31)=7.74 P=.009). While P3 in response to pure tones was lower than P3 in response to tones concurrently presented with pictures in case of ignore session (F(1,31)=2.92 P=.097), opposite difference was observed in count session where P3 in auditory+visual condition was diminished in comparison to P3 in auditory condition (F(1,31)=2.99 P=.094).

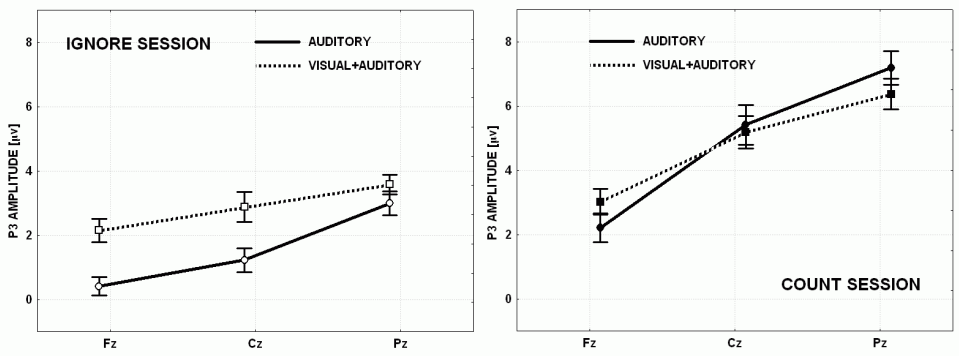


Figure 2. Mean amplitudes of auditory P3 (± SEM) as a function of electrode location obtained in ignore (upper panel) and count (lower panel) sessions. Solid line represents auditory condition and dashed line represents visual+auditory condition.

**Latencies of auditory P3**

Latencies of the P3 deflection observed in auditory condition increased from frontal to parietal locations, however this effect did not reach the level of significance (F(2,62)=2.80 P=.069 ε=.941) and similar pattern was obtained for both ignore and count sessions (effect of SESSION F(1,31)=0.09 P>.05; interaction SESSION × LOCATION F(2,62)=1.54 P>.05 ε=.932) as indicated in Figure 3. In contrast to this, latencies of P3 recorded in response to tones accompanied with visual stimuli show the opposite pattern. The shortest latencies were measured on parietal sites while the longest on frontal sites (F(2,62)=7.85 P<.001 ε=.996), and again, similar pattern was obtained for both ignore and count sessions (effect of SESSION F(1,31)=1.49 P>.05; interaction SESSION × LOCATION F(2,62)=0.04 P>.05 ε=.877). This leads to significant interaction CONDITION × LOCATION when analysis is performed across sessions (F(2,62)=7.85 P<.001 ε=.995). Moreover, significant main effect of CONDITION was also obtained (F(1,31)=4.33 P<.05). Similar

significant CONDITION × LOCATION interaction, were also found when analyses were performed separately for ignore and count session ($F(2,62)=4.74$ $P=.018$ $\varepsilon=.830$ and $F(2,62)=4.49$ $P=.025$ $\varepsilon=.753$, respectively). However, main effect of CONDITION was found insignificant in separate analysis for ignore and count sessions ($F(1,31)=2.90$ $P>.05$ and $F(1,31)=1.25$ $P>.05$ respectively).

**Amplitudes of visual P3**

Figure 4 shows the grand average ERP elicited by pictures presented as the visual background in both the ignore and count sessions. P3 component was clearly visible mainly at parietal sites while in other cases was less evident. The analysis showed that P3 has a typical maximum over parietal locations (main effect of LOCATION $F(2,62)=43.92$ $P<.0001$ $\varepsilon=.591$), what is indicated in Figure 5. The same pattern was also evident when the analysis was separately done for ignore session ($F(2,62)= 50.59$ $P<.0001$ $\varepsilon=.618$) as well as for count session ($F(2,62)=30.98$ $P<.0001$ $\varepsilon=.598$). This suggests that the amplitudes of the visual P3 component obtained in both sessions increased from frontal to parietal locations. No significant difference between sessions was found (main effect of SESSION $F(1,31)=1.18$ $P>.05$). Analysis of SESSION × LOCATION interaction also brought no significant result ($F(2,62)= 0.20$ $P>.05$ $\varepsilon=.618$). These results suggest that visual stimulation evoked similar brain responses in both sessions of the experiment.

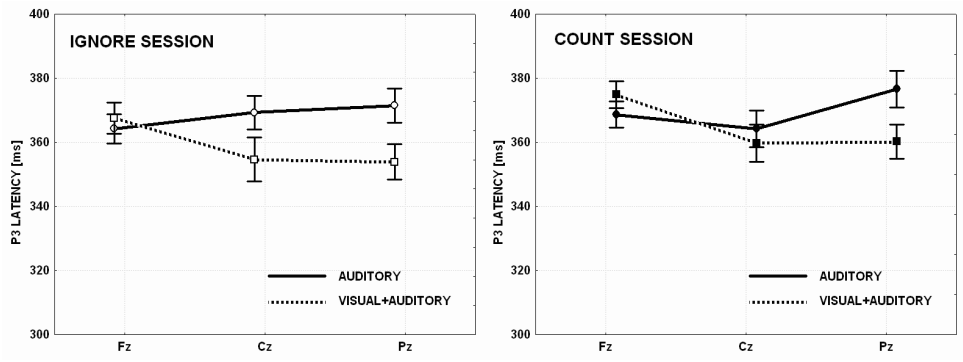


Figure 3. Mean latencies of auditory P3 (± SEM) as a function of electrode location obtained in ignore (upper panel) and count (lower panel) sessions. Solid line represents auditory condition and dashed line represents visual+auditory condition.

**Latencies of visual P3**

Latencies of the visual P3 deflection observed across sessions increase from parietal to frontal locations (main effect of LOCATION $F(2,62)=19.86$ $P<.0001$ $\varepsilon=.982$), similar pattern was obtained for both ignore and count sessions ($F(2,62)=15.07$ $P<.0001$ $\varepsilon=.989$ and $F(2,62)=9.80$ $P<.0003$ $\varepsilon=.957$, respectively) what is illustrated in Figure 6. The latencies of visual P3 recorded in count session were slightly longer than the latencies of P3 obtained in ignore session (main effect of SESSION $F(1,31)=5.63$ $P=.024$). At least, analysis of SESSION × LOCATION interaction brought no significant result ($F(2,62)= 0.12$ $P>.05$ $\varepsilon=.985$) what confirms our previous suggestion that visual stimulation evoked similar brain responses in both sessions.

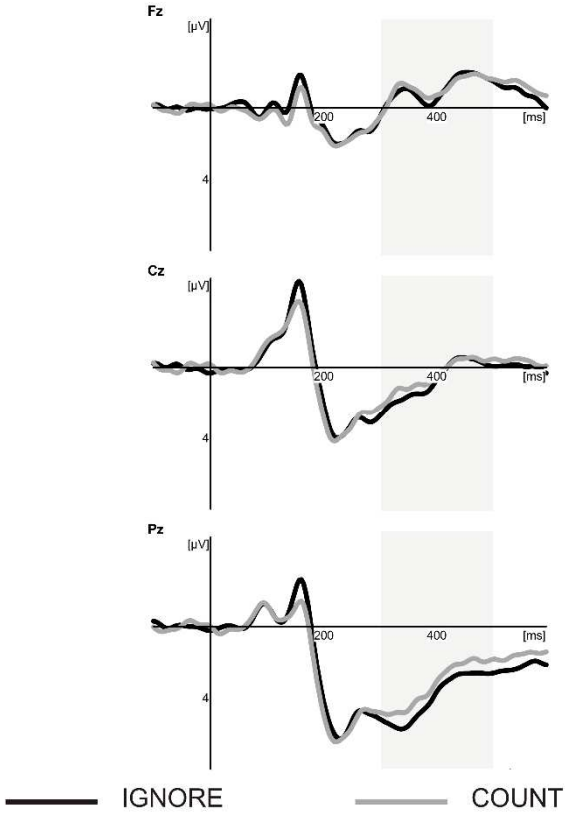


Figure 4. Grand average visual ERP recorded in ignore (black lines) and count (grey lines) sessions. The latency window of the P3 component (300-500 ms poststimulus) is highlighted.

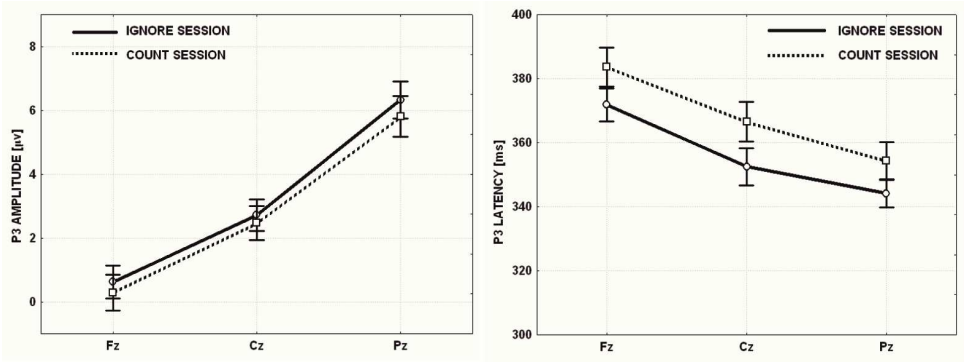


Figure 5. Mean amplitudes (left panel) and mean latencies (right panel) of visual P3 (± SEM) as a function of electrode location obtained in ignore (solid line) and count (dashed line) sessions.

## Discussion

The differential amplitude of the parietal P3 in ignore and count session confirmed the successful manipulation of the task instruction. When participants were informed that subsequent stimuli were irrelevant and no response was required, the response to auditory stimuli alone consisted of a small P3-like component obtained over both the parietal and the frontal location. On the contrary, when voluntary attention resources were provoked by the experimental instruction, a significantly larger auditory P3 response was produced over the parietal location, along with an increase of the P3 amplitude at the frontal site. This effect of attention engagement was evident both when tones were or were not accompanied by visual stimuli. However, the processing of auditory events was crossmodally influenced by visual stimulation. When ignore task was employed, additional visual stimulation produced a change in the amplitude of the frontal P3 component but not of the parietal P3. Different pattern of modulation was observed when an involuntary attention shift was produced by the exposition to additional visual stimuli during count task. In this case, the amplitude of frontal P3 evoked in response to subsequently presented auditory stimuli was also increased, while at the same time, the parietal P3 amplitude was diminished in comparison to the P3 amplitude to tones alone observed during the count task.

The effect of additional exposition to visual stimuli differed between the passive and active condition. In the passive condition (ignore session), the crossmodal influence of additional visual stimuli exposition was restricted to a change in the magnitude of the frontal response to tones, but in the active condition (count session), a similar alteration

over anterior location co-existed with an additional change in the amplitude of the parietal P3 response to tones. In this case, the direction of the observed shifts in ERP was actually opposite. Simultaneously, the latency of P3 component was shortened by additional visual stimulation in both passive and active sessions.

The presentation of visual stimuli boosted the amplitude of auditory P3 measured over anterior locations. An increased frontal P3 may therefore stem from frontal lobe responses to visual stimuli presented shortly before. The presentation of pictures could involuntary engage the frontal lobe and, consequently, increase initial attention allocation (Posner and Petersen, 1990). Subsequently presented auditory stimuli could therefore evoke a stronger frontal lobe response reflected in an enhanced frontal P3, in comparison to auditory stimuli presented alone. This effect was observed irrespective of the experimental instruction, in both ignore and count session. Thus, attention to stimuli presented in one modality could change the subsequent frontal response to neutral stimuli in another modality. This is consistent with Näätänen's suggestion that P3a could be regarded as a reflection of the attentional switch produced from the mismatch between stimulus properties and the previously passively formed neuronal trace (Näätänen, 1990). The frontal P3 was also significantly enhanced as the consequence of, presumably, a greater attentional focus in the active condition. This effect was obtained when tones became relevant by the experimental instruction, which is supposed to evoke controlled processing. This finding is consistent with previously reported data (Comerchero and Polich, 1999; Katayama and Polich, 1998), suggesting a relationship between the strength of an attentional focus and the magnitude of the P3a response. According to the task performed by the our subjects, a greater attentional focus in the active condition was expected, and as the outcome of attention engagement an increased frontal P3 was observed. In addition, the results provided evidence that both types of frontal responses, the involuntary shift in reaction to neutral pictures and the voluntary focus provoked by the instruction, are capable to increase the frontal P3 amplitude. Moreover, the present data support the thesis that these two effects could be, at least partially, additive.

The results presented here provide further evidence that a controlled processing of auditory stimuli could be diminished when visual material is simultaneously presented. The effects of the experimental manipulation seen in P3, reflects the evaluation of auditory events. However, the preceding exposition to slides diminished the P3 amplitude, which is considered as a correlate of the voluntary evaluation process mentioned above. The perceptual processing of the pictures and the subsequent involuntary attention shift, require extra attentional resources, which cannot be devoted easily to the controlled processing of auditory stimuli. Thus, the processing of the relevant tones is negatively crossmodally affected by the processing of the simultaneously

presented pictures, and this effect is reflected in a diminished P3. This is consistent with previous findings of Schupp et al. (1997) and Cuthbert et al. (1998), who obtained a similar influence of neutral and emotionally-relevant pictures on the processing of either tones or startling stimuli. They found that the P3 response was smaller when auditory stimuli were exposed on an emotionally arousing background, as compared to a neutral background. The conclusion was that a reduction in the auditory P3 amplitude reflects a greater allocation of attentional resources to more demanding stimulation. Comparable findings were also reported by Oray et al. (2002), who obtained a reduced auditory P3 amplitude in response to tone bursts presented along with pictures, in comparison to tones alone. Reduction of auditory P3 response observed in our study is also compatible with the findings of other researches (Michalski, 2001; Milner and Michalski, 2003), who suggested that cortical responsiveness to irrelevant stimulation is reduced during P3 potential. They found that early stages of visual processing could be affected when stimuli presented shortly before are engaging attention.

## Conclusions

In conclusion, auditory stimuli evoked a P3 component of different magnitude over frontal and parietal locations. This was mediated both by attention demands and by parallel processing of visual stimuli. In particular, the P3 recorded over the parietal cortex was strongly dependent on the cognitive load. When attention was voluntarily allocated to relevant stimuli evident P3 was obtained. However, parallel visual processing could decrease the strength of this effect. Thus, a parietal P3 could be affected crossmodally by an involuntarily attention shift to visual stimuli and this effect represents allocation of attention resources. The frontal P3 was found to be related to involuntary (or voluntary) attention shift. Increases in P3 amplitude on frontal locations were obtained in two conditions: a) when auditory stimuli had to be counted by the subjects (voluntary shift), and b) when attention was directed to visual stimuli and unexpectedly tones were presented (involuntary shift). These results lead to the suggestion that the involuntary processing of visual stimuli might crossmodally change the processing of auditory stimuli. This effect could be observed not only when the perceived stimuli have a special affective meaning, but even when the stimuli are neutral. However, this deficit in allocation of attentional resources was restricted to the active condition only, when the matching of a template with incoming information results in a distinct P3 component. The possible source of the effect is a change in the frontal cortex activity. Frontal neurons project to more posterior parts of the brain, such as the inferior temporal cortex and parietal cortex (Yamaguchi and Knight, 1991b). Single-cell recordings in animals and neuroimaging

studies in humans, provide evidence that the dorsolateral prefrontal cortex is important for holding temporary representations in working memory. The presentation of visual pictures evokes activity in the anterior attention system, reflecting the involuntary processing of new templates in working memory. Another template is created as the result of the experimental instruction to count the auditory stimuli during the active session. Both processes, which can also occur independently, cause a change in the activity of the frontal cortex, and this is expressed in an increased P3a amplitude.

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# CHAPTER 3

## The auditory P3 from passive and active three-stimulus oddball paradigm *

**Abstract**

The aim of this study was the comparison of basic characteristics of the P3 subcomponents elicited in passive and active versions of the auditory oddball paradigm. A 3-stimulus oddball paradigm was employed in which subjects were presented with random sequence of tones while they performed a discrimination task in visual modality with no response to the tone (passive task) or responded to an infrequently occurring target stimulus inserted into sequence of frequent standard and rare non-target stimuli (active task). Results show that the magnitude of the frontal P3 response is determined by the relative perceptual distinctiveness among stimuli. The amplitude of frontal component is larger for the stimuli more deviated from the standard in both passive and active tasks. In all cases however, a maximum over central or fronto-central scalp regions was demonstrated. Moreover, amplitude of this component was influenced by the strength of attentional focus. A significantly larger response was obtained in the active session than in its passive counterpart. The apparent parietal P3 responses were obtained only in the active condition. The amplitude of this component is larger for the target than the non-target across all electrode sites, but both demonstrated the parietal maxima. This findings suggest that generation of early frontal P3 could be related to alerting activity of frontal cortex irrespective of stimulus context, while generation of later parietal P3 is related to temporo-parietal network activated when neuronal model of perceived stimulation and attentional trace are comparing.

### Introduction

The P3 is probably the most frequently studied component of the Event-Related Potentials (ERP). It has been widely applied in studies of cognitive dysfunction in clinical population as well as normal functioning in healthy subjects (Polich and Herbst, 2000; Hruby and Marsalek, 2003). There is general agreement that P3 provides a valuable tool

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for the systematic investigation of attentional and memory processes in the human brain. This positive component, with a peak latency of 300–800 ms, is commonly obtained in several versions of the oddball paradigm (Picton, 1992; Polich and Kok, 1995; Comerchero and Polich, 1999). In this paradigm, rare target stimuli are inserted in series of much more frequent standard stimuli of the same modality. The task given to the subject is usually to notice the presence of target stimulus and to react to it, typically by pressing a button, or just by mental counting. P3 responses with a similar topography can also be generated in a single stimulus task where a single target is randomly presented as in the oddball paradigm, but with the standard stimuli replaced by silence (Polich et al., 1994; Mertens and Polich, 1997; Strüber and Polich, 2002; Wronka et al. 2007). In the 3 stimulus variant of the oddball paradigm, an additional infrequent non-target stimulus is inserted into a sequence of infrequent target and frequent standard stimuli (Katayama and Polich, 1998; 1999). In contrast to this, the passive version of oddball task does not require reaction from the subject. In this case, subject's attention is usually directed away from the sequence of standard and deviant tones toward another, moderately demanding task, usually in different modality (Näätänen, 1990).

There is general consensus that P3 is not a unitary brain potential but represents the summation of activity from various widely distributed areas in the brain and a distinction can be made between several subcomponents which temporally overlap (Polich and Criado, 2006). It is generally accepted that a distinction can be made between at least two subcomponents, namely the P3a and the classical P3 (or P3b). The P3a is a large, positive deflection with a fronto-central distribution and is typically elicited by novel or non-target stimuli inserted in a series of standard and target stimuli in a 3 stimulus oddball paradigm. This component has a relatively short peak latency (Courchesne et al., 1975; Friedman and Simpson, 1994). A suggestion is that it reflects an alerting process in the frontal lobe while involuntary attention shifts to changes in the environment takes place (Yamaguchi and Knight, 1991a). The P3a is sometimes referred to as the novelty P3 (Yamaguchi and Knight, 1991a; 1991b). However, it is still not clear if the P3a and 'novelty' P3 reflect exactly the same physiological and psychological process even if they share similar scalp topography (Courchesne et al., 1975; Squires et al., 1975).

The P3b (or classical P3) has a more posterior-parietal scalp distribution and a somewhat longer latency than P3a. There is broad evidence that this component could be regarded as reflecting target stimulus classification in tasks that require some form of action like a covert or overt response to stimuli (Donchin and Coles, 1988; Kok, 2001). Specifically, the P3b has been considered as indexing voluntary attention, such that its amplitude reflects the allocation of attentional resources (Kok, 2001; Wronka et al., 2007), and its peak latency is considered to be related to stimulus evaluation time (Kutas et al., 1977). What also important is that, the distinction between P3a and P3b is evident

for both auditory and visual modalities (Comerchero and Polich, 1999; Katayama and Polich, 1999). The P3b component seems to be elicited exclusively by target stimulus, the only stimulus in the sequence required obligatory response. In contrast to this, rare but non-target visual stimuli which could be easily recognized elicit a P3 with maximum over central-parietal areas (Courchesne, 1978; Courchesne et al., 1978). Similarly, in the auditory modality, Pfefferbaum and colleagues (1980; 1984) found that an infrequently presented non-target tone inserted into the traditional oddball tone sequence elicited a parietal P3 of smaller amplitude than the target P3. This component is sometimes referred to as a 'no-go' P3 since response to infrequent non-target is not required from the subject.

When taken together with the P3a subcomponent findings outlined above, it could be suggested that the P3 may be composed of at least few constituent potentials that reflects distinct information processing events. Thus, all the P3 subcomponents appears to vary in their locus of scalp distribution, magnitude and peak latency as a function of the stimulus context. There is no agreement for naming the P3 subcomponents elicited in a passive condition, physically novel stimuli, or rare non-target stimuli in three-stimulus oddball task, whereas a target P3 from the active tasks is consistently referred to as P3b. Näätänen (1990) has suggested that P3a could be considered as the reflection of the attentional switch produced from the mismatch between a presented stimulus and passively formed neuronal trace, whereas P3b reflects the match between the stimulus and voluntarily maintained attentional trace.

The purpose of the present study was to examine in more detail the basic characteristics of the P3 subcomponents elicited in the passive and active versions of the three-tone oddball paradigm. As it was outlined above, the three-stimulus oddball paradigm is a modification of the oddball task in which rare non-target stimuli are inserted into a sequence of rare target and frequent standard stimuli (active version) or two different rare stimuli are presented in addition to the sequence of more frequent standard stimulus (passive version). In its passive variant the three-stimulus paradigm gives the opportunity to verify the finding that the relative perceptual distinctiveness among stimuli significantly affects the amplitude of the early fontal P3a. The greater is the mismatch between the standard and rare stimuli (usually dubbed as deviant stimuli) the stronger the attentional switch and the larger is the P3a response to the presented deviant. At the same time, however, no specific reaction is required from the subject and thus, no evident P3b component would be expected in reaction to deviant stimuli exposition. The active variant of three-stimulus oddball task could also be utilize to elicit the P3a response (Katayama and Polich, 1998; 1999; Comerchero and Polich, 1999; Jeon and Polich, 2001) which is not readily apparent in all individuals when traditional two-stimulus oddball is implemented (Polich, 1988). If the P3a component, elicited under

passive and active conditions, reflects similar physiological processes, then its scalp distribution as well as the relative difference dependent on stimulus distinctiveness, will not differ significantly. However, studies in which characteristics of this component have been directly compared between passive and active condition are scarce (Bennington and Polich, 1999; Jeon and Polich, 2001). It could be also noticed that in most studies with three-stimulus tasks no differentiation were made between the early and late P3 (Katayama and Polich, 1996a; 1996b; 1998; 1999; Comerchero and Polich, 1999; Jeon and Polich, 2001). Hence, so far it is not clear whether early frontal P3s obtained in passive and active condition reflect similar physiological processes. In the active three-stimulus paradigm an obvious P3 with parietal maximum should be obtained in response to both target and non-target stimuli. However, also in this case, it is not clear whether both differ in its scalp distribution and thus reflect activity of distinct brain generator.

Taken together, our experimental design allow a direct comparison of basic characteristics of both frontal and parietal P3 components measured in response to exactly the same set of auditory stimuli under passive and active conditions. We predict that if early frontal P3a components measured under passive and active tasks in our experiment will not differ significantly in their scalp topography then both reflect the same or a very similar physiological and psychological process. At the same time we expect differences in their amplitudes which are determined by the strength of attentional focus (Katayama and Polich, 1999). Similarly, if the late parietal P3 components obtained in response to target and non-target stimuli in active task will not differ in their scalp distribution, despite the expected differences in its amplitude and latency, then both could be considered as the index of a similar set of processes. In order to determine clearly the P3 subcomponents, difference waves were calculated by subtracting the standard stimulus ERP from both deviants' stimuli ERPs obtained in passive condition and from both target and non-target ERPs obtained in active condition.

## Methods

### Subjects

Thirty healthy male and female students (M = 21.1 years; SD = 1.52 years) served as participants in the experiment. All of them were right-handed and had normal, or corrected to normal, vision, as well as normal hearing. They received course points for their participation and signed an informed consent. All participants, reported being free of neurological or psychiatric disorders. Due to excessive eye or muscle artefacts two subjects had to be excluded, thus the final group consisted of twenty eight subjects (20 females and 8 males).

**Recording conditions**

The EEG was recorded from 31 mono-polar locations (Fp1/Fp2, F3/F4, F7/F8, FT7/FT8, FC3/FC4, T7/T8, C3/C4, TP7/TP8, CP3/CP4, P7/P8, P3/P4, O1/O2, AFz, Fz, FCz, Cz, CPz, Pz, Oz) according to the 10.20 international electrode placement system. All the electrodes were placed on the scalp using an Electro-Cap and were referred to the C1 recording. The horizontal and vertical EOG were monitored by additional 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. The EEG was amplified at a sampling rate of 1024 Hz using BioSemi ActiveOne system. Output data were subsequently transferred to and stored in a computer for analysis. The EEG data was off-line filtered with band pass 0.01–35 Hz (24 dB), and sampled for 1.0 s trial (100 ms prior to stimulus onset and 900 ms after stimulus onset) using BrainVision software. Finally, data were corrected for eye-movement artifacts (Gratton et al., 1983) and rereferenced to average montage.

**Procedure**

The entire experiments lasted about one hour, interrupted by a short break, and subjects were seated in a darkened sound-isolated, air-conditioned chamber. They were asked to relax and to restrict body movements and blinking as much as possible. Two separate sessions in the experiment were employed. In the first session the subjects were presented with random series of tones (consisting of standard, deviant 1 and deviant 2 tones with probabilities of 0.80, 0.10, and 0.10, respectively) while they performed visual task. In the visual task, random series of photographs of faces were presented and subjects were instructed to silently count the male or female faces (this instruction was counterbalanced across the subjects). They were also informed that there was no task associated with the auditory stimuli. In the second session the subjects were only presented with random series of tones (consisting of standard, target and non-target tones with probabilities of 0.80, 0.10, and 0.10, respectively) and were asked to silently count the target tones and report the total number at the end of the session. The passive condition was introduced to each participant before they undertook the active condition. The fixed order of the tasks was used to avoid the carry-over effect possible when a set of stimuli attended in one condition should be ignored in the following condition.

| stimulus type<br>passive condition (probability) | stimulus type<br>active condition (probability) | frequency |
|---|---|---|
| standard (.80) | standard (.80) | 1000 Hz |
| deviant 1 (.10) | target (.10) | 1100 Hz |
| deviant 2 (.10) | non-target (.10) | 1200 Hz |

Table 1. Probabilities and frequencies (Hz) for each stimulus type and experimental condition.

**Stimuli**

Stimulus tones were presented with random ISI (1.25.2.0 s) through loudspeaker located in front of subject at 65 dB SPL (100 ms duration with 10-ms rise/ fall time). The tone frequencies for each stimulus type and experimental condition are summarized in Table 1.

The visual stimuli in passive condition were presented on a 19 inch monitor viewed from a distance of 1 m. Stimuli were centrally presented black and white photographs (10 × 15 cm) of 10 different individuals (5 women and 5 men) with neutral facial expression. Each visual stimulus was presented for 6 s with random ISI (4.8 s). The onset of visual stimuli was always simultaneous to the onset of standard auditory stimulus and these trials were excluded from analysis.

**Data analyses**

The P3 latencies and amplitudes were measured on difference waves, calculated by subtracting the average ERP elicited by the standard stimuli from that elicited by the deviant 1 (target) and deviant 2 (non-target) stimuli. As the focus of the present study was the basic characteristics of the P3 components elicited in response to rare stimuli (deviant 1/target; deviant 2/non-target), only the P3s from these stimuli are reported. The components are defined as the largest positive-going peaks within a specific latency window: for the passive condition 200-350 ms and 350-700 ms for the early and late P3s, respectively, and for the active condition 250-400 ms and 400-700 ms for the early and late P3s, respectively. These windows were selected on the basis of visual inspection of grand averaged ERP obtained for each condition. Peak amplitude was calculated relative to the pre-stimulus baseline, and peak latency was measured from the time of stimulus onset.

Repeated-measures analyses of variance (ANOVA) were performed examining the effect of within-subjects factors of electrodes LOCATION (5 anterior-to-posterior locations), STIMULUS type (deviant 1/target vs. deviant 2/non-target), and CONDITION (passive vs. active) on P3 mean amplitude and latency. The effects of LOCATION were examined in orthogonal five-level repeated-measures sagittal factor and arranged such that the lateral (coronal) electrode arrays were nested under the anterior-to-posterior factor locations (F3-Fz-F4 vs. FC3-FCz-FC4 vs. C3-Cz-C4 vs. CP3-CPz-CP4 vs. P3-Pz-P4), which yielded two orthogonal electrode factors. This approach permits the direct assessment of interactions between the frontal-to-parietal topography distributions across lateral electrode with respect to the experimental independent variables. All analyses of variance employed Greenhouse-Geisser corrections to the degrees of freedom when appropriate, and only the corrected probability values are reported. The Bonferroni method was used for *post-hoc* comparisons, with a significance level of 0.05.

## Results

Task performance was virtually perfect for both conditions (<1% error rates for each condition).

Figure 6 presents the grand average ERPs from the standard, deviant 1, and deviant 2 stimuli for each electrode under passive condition. Figure 7 presents the grand average ERPs from the standard, target, and non-target stimuli for each electrode under active condition. Difference waves from passive condition obtained by subtracting ERP for standard tone from ERPs for both deviant 1 and deviant 2 stimuli is presented in Fig. 9. Similarly, difference waves from active task, acquired by subtracting standard stimulus ERP from ERPs for target and non-target tones, is represented in Fig. 10.

### Early P3 amplitude

The mean P3 amplitudes from the passive condition (deviant 1 and deviant 2 stimuli) and from the active condition (target and non-target stimuli) are illustrated in Fig. 11. The data were assessed initially with a three-factor (LOCATION × CONDITION × STIMULUS) ANOVA. The results of this analysis are summarized in Table 2, in which only significant effects are presented. The amplitude of P3 component measured during active condition was significantly larger when compared to the P3 obtained in passive condition. On the other hand, significantly larger P3 amplitude was observed in response to rare stimuli more physically deviated from standard stimulus (deviant 2 and non-target), in comparison to P3 elicited by deviant 1 or target stimuli. This effect was comparable for passive and active condition what is confirmed by insignificant STIMULUS × CONDITION interaction.

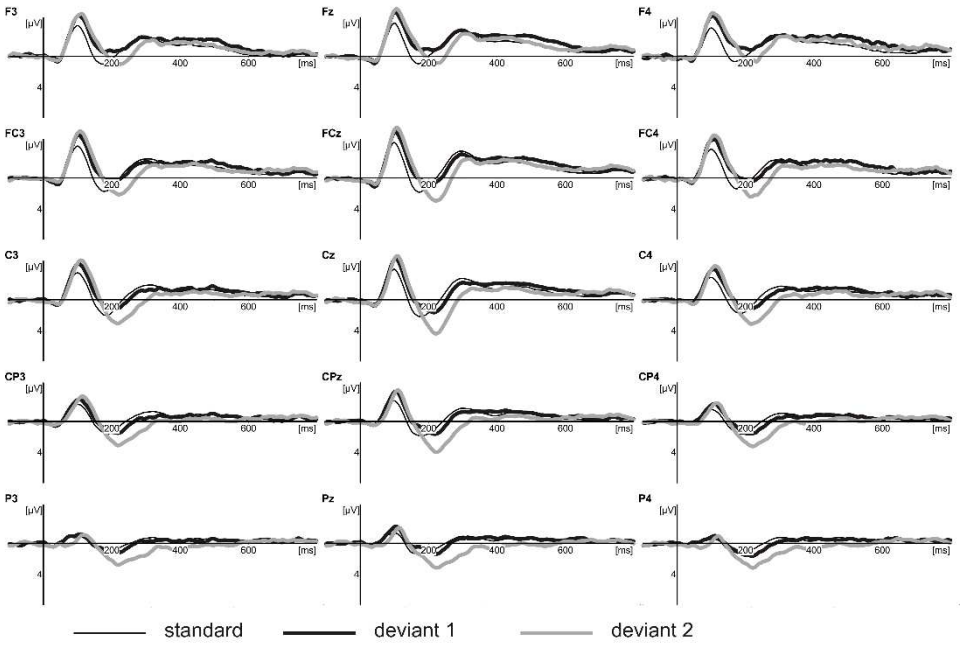


Figure 6. Grand averaged ERP recorded in passive condition for each stimulus type and recording site. Thin black lines represent responses to standard stimuli, black thick lines indicate responses to deviant 1 stimuli and grey lines represent responses to deviant 2 stimuli.

Because the three-way interaction was significant, separate two-factor (LOCATION × STIMULUS) analyses on passive and active conditions were performed. The main effect of stimulus type was still significant in both analyses ($F(1,27)=16.80$, $P<0.001$ and $F(1,27)=9.74$, $P=0.004$, for passive and active condition respectively). The amplitude of P3 recorded in response to deviant 2/non-target stimuli was found bigger in comparison to P3 obtained in response to deviant 1/target tones. This suggests that the magnitude of P3 response is related to the size of rare stimuli deviation from standard tone. Similarly, the main effect of location was significant in both analyses either ($F(4,108)=6.3,1$ $P=0.010$, $\varepsilon=0.340$ and $F(4,108)=4.05$, $P=0.031$, $\varepsilon=0.413$, for passive and active condition respectively). For the passive condition, the P3 of maximal amplitude was recorded at the Cz electrode for both deviant stimuli. In contrast to this, for the active condition maximum at Cz was obtained for the non-target stimuli whereas the P3 elicited by the target stimulus peaked maximally at more anterior FCz electrode. This leads to a significant

interaction of LOCATION × STIMULUS factors for active ($F(4,108)=11.37$, $P<0.001$, $\varepsilon=0.437$) but not or passive condition.

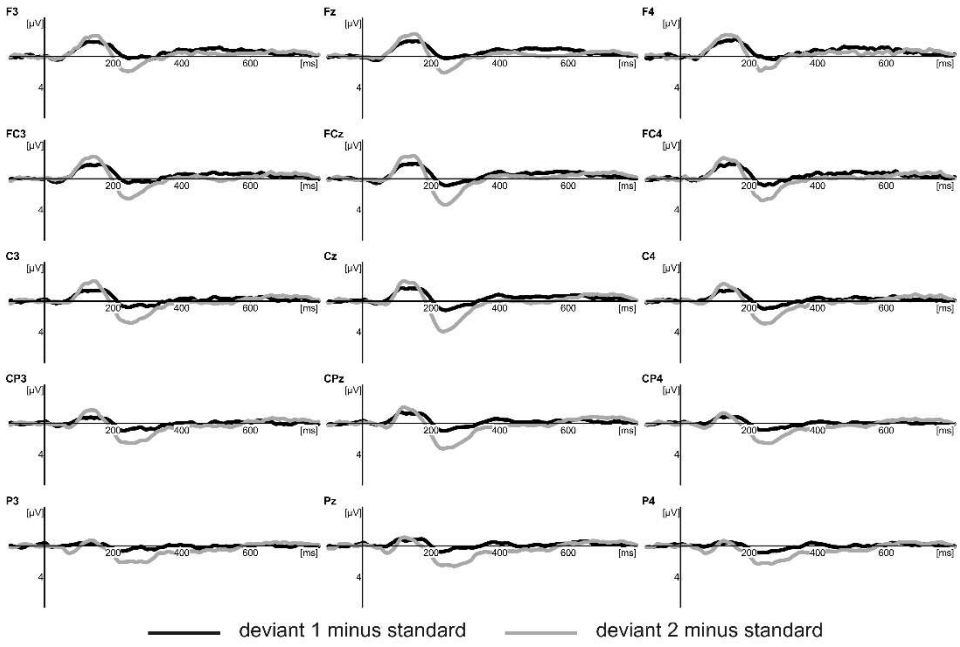


Figure 7. Grand averaged difference waves calculated for passive condition for each stimulus type and recording site. Black lines represent deviant 1 minus standard difference and grey lines represent deviant 2 minus standard difference.

**Late P3 amplitude**

The mean P3 amplitudes from the passive condition (deviant 1 and deviant 2 stimuli) and from the active condition (target and non-target stimuli) are illustrated in Fig. 10. The data were assessed initially with a three-factor (LOCATION × CONDITION × STIMULUS) ANOVA. The results of this analysis are summarized in Table 2, in which only significant effects are presented.

The amplitude of P3 component measured during active condition was significantly larger in comparison to the P3 recorded in passive condition. Main effect of STIMULUS was not significant. However, at the same time, significant STIMULUS × CONDITION interaction was found. The P3 amplitude in response deviant 2 stimuli under passive condition was larger than P3 amplitude obtained for deviant 1 tones. An opposite

difference was observed in the active condition where P3 elicited by target tones was larger in comparison to P3 elicited by non-target stimuli as it is indicated in Fig. 10. Finally, no significant result was found when the three-way interaction (LOCATION × CONDITION × STIMULUS) was examined.

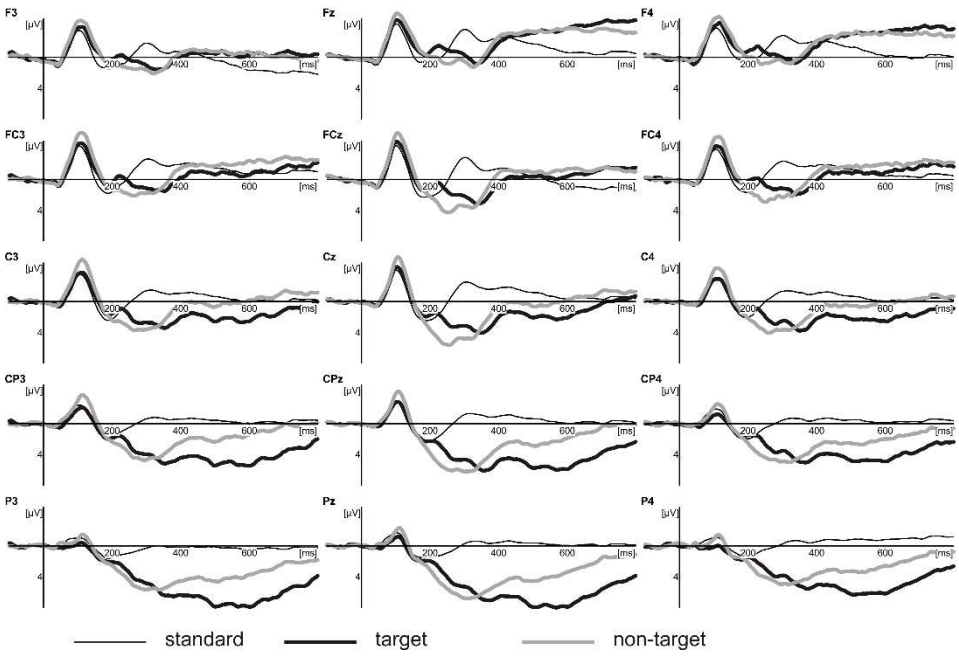


Figure 8. Grand averaged ERP recorded in active condition for each stimulus type and recording site. Thin black lines represent responses to standard stimuli, black thick lines indicate responses to target stimuli and grey lines represent responses to non-target stimuli.

When an analysis of the effect of LOCATION was separately done for each condition, a significant results were found for both the passive ($F(4,108)=7.77$, $P=0.002$, $\varepsilon=0.432$), and for the active task ($F(4,108)=36.20$, $P<0.001$, $\varepsilon=0.329$). This suggests that the amplitude of the late P3 component, obtained in both conditions and for both types of rare stimuli, increased from frontal to parietal locations. This suggestion was additionally confirmed by non-significant interaction STIMULUS × LOCATION for both passive and active condition. Finally, an analysis of the effect of STIMULUS separately conducted for each condition delivered a significant result but only for P3 obtained in active condition ($F(1,27)=10.32$, $P=0.003$), but not for its passive counterparts.

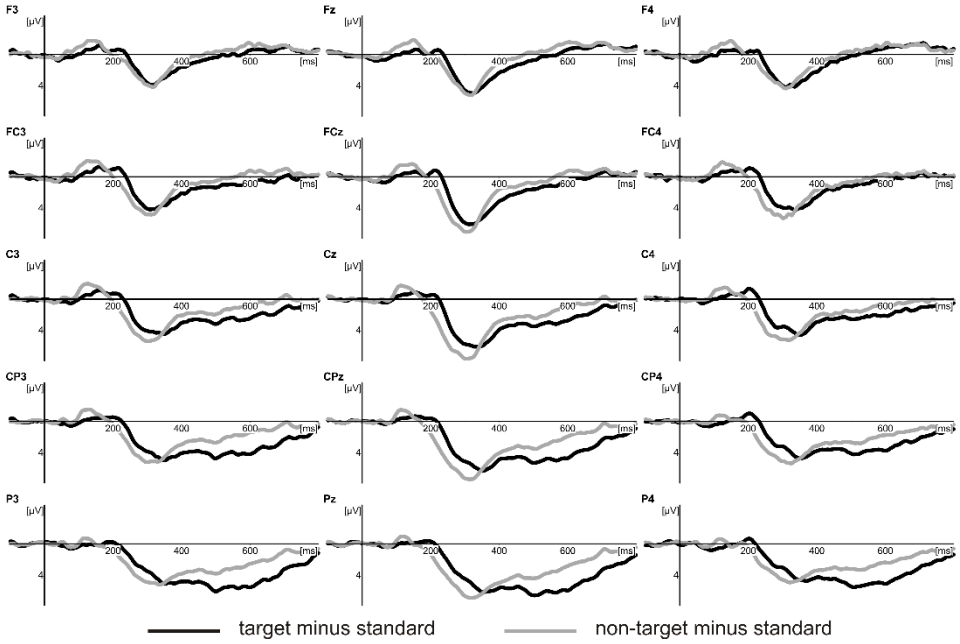


Figure 9. Grand averaged difference waves calculated for active condition for each stimulus type and recording site. Black lines represent target minus standard difference and grey lines represent non-target minus standard difference.

**Early P3 latency**

The mean P3 latencies from the passive condition (deviant 1 and deviant 2 stimuli) and from the active condition (target and non-target stimuli) are illustrated in Fig. 11. The data were assessed initially with a three-factor (LOCATION × CONDITION × STIMULUS) ANOVA. The results of this analysis are summarized in Table 3, in which only significant effects are presented. Highly significant main effect of CONDITION was found indicating that latencies of early P3 components measured in passive condition were shorter than of the equivalent peaks in active condition. Moreover, latency of P3 response to deviant 2 stimulus was shorter than latency of P3 component measured as a response to deviant 1 stimulus. Comparable effect was observed also for active condition, where latency of P3 component elicited by non-target tone was shorter than latency of target P3. This leads to significant main effect of STIMULUS. However, strength of this effect was varied between anterior and posterior location, which resulted in a significant interaction of STIMULUS × LOCATION factors. No other effects or interaction were significant.

| | early P3 amplitude | | | late P3 amplitude | | |
|---|---|---|---|---|---|---|
| Source (df) | F | P | ε | F | P | ε |
| LOCATION (4,108) | 6.62 | .007 | .372 | 35.10 | <.001 | .319 |
| STIMULUS (1,27) | 19.20 | <.001 | - | - | - | - |
| CONDITION (1,27) | 23.04 | <.001 | - | 23.31 | <.001 | - |
| STIMULUS × CONDITION (1,27) | - | - | - | 13.19 | .001 | - |
| LOCATION × STIMULUS (4,108) | 8.31 | .002 | .369 | - | - | - |
| LOCATION × CONDITION (4,108) | - | - | - | 28.07 | <.001 | .374 |
| LOCATION × STIMULUS × CONDITION (4,108) | 4.10 | .031 | .405 | - | - | - |

Table 2. Summary of the three-factor analysis of variance on the early and late P3 amplitudes.

When the interaction of STIMULUS × LOCATION was inspected separately for each condition, a significant results were found for both the passive ($F(4,108)=4.16$, $P=0.011$, $\varepsilon=0.551$), and for the active task ($F(4,108)=5.40$, $P=0.003$, $\varepsilon=0.656$), what confirmed our previous conclusion. At the same time, significant effect of STIMULUS was obtained for passive condition ($F(1,27)=6.81$, $P=0.015$). In case of similar analysis performed for active condition this effect did not reach the level of significance ($F(1,27)=2.93$, $P=0.098$). No other effects were significant.

**Late P3 latency**

The mean P3 latencies from the passive condition (deviant 1 and deviant 2 stimuli) and from the active condition (target and non-target stimuli) are illustrated in Fig. 11. The data were assessed initially with a three-factor (LOCATION × CONDITION × STIMULUS) ANOVA. The results of this analysis are summarized in Table 3, in which only significant effects are presented. Significant main effect of CONDITION was found indicating that latency of P3 component measured in active condition was shorter than the latency of P3 peak in passive condition. This difference was especially clear for anterior location, what was confirmed by significant interaction of LOCATION × CONDITION. At the same time, the three-way interaction (LOCATION × STIMULUS × CONDITION) was also significant.

| | early P3 latency | | | late P3 latency | | |
|---|---|---|---|---|---|---|
| Source (df) | F | P | E | F | P | ε |
| LOCATION (4,108) | - | - | - | - | - | - |
| STIMULUS (1,27) | 11.48 | .002 | - | - | - | - |
| CONDITION (1,27) | 49.86 | <.001 | - | 5.69 | .024 | - |
| STIMULUS × CONDITION (1,27) | - | - | - | - | - | - |
| LOCATION × STIMULUS (4,108) | 9.71 | <.001 | .622 | - | - | - |
| LOCATION × CONDITION (4,108) | - | - | - | 12.92 | <.001 | .619 |
| LOCATION × STIMULUS × CONDITION (4,108) | - | - | - | 5.40 | .002 | .730 |

Table 3. Summary of the three-factor analysis of variance on the early and late P3 latencies.

When the separate two-factor (LOCATION × STIMULUS) analyses on passive and active conditions were performed for each condition, a significant result was found only for the active condition ($F(4,108)=4.16$, $P=0.013$, $\varepsilon=0.626$). Simultaneously, inspection of effect of LOCATION delivered significant results for both passive ($F(4,108)=3.78$, $P=0.025$, $\varepsilon=0.548$) and active condition ($F(4,108)=7.74$, $P=0.001$, $\varepsilon=0.572$). The weak effect of STIMULUS was observed only in active condition and did not reach the level of significance ($F(1,27)=3.12$, $P=0.089$).

## Discussion

The differential amplitudes of the late parietal P3 measured in response to both nonstandard in the passive and active session confirmed the successful manipulation of the task instruction. When participant's attention was engaged in the visual task and no specific reaction to auditory stimuli was required, the ERP measured in response to both deviant stimuli consisted of small deflection observed in P3 time window with a maximum over the parietal location. On the contrary, when voluntary attention resources were provoked by experimental instruction to discrimination among auditory stimuli evident P3 deflections were obtained for both target and non-target stimuli. In both cases, parietal maxima were observed. It is also reasonable to conclude that the target and non-

target stimulus in the auditory modality elicited a P3 component with the same neural generator. This finding extend previous results of Katayama and Polich (1999), in which normalized amplitude analysis indicated that the topography of the P3 component measured in auditory and visual three-stimulus tasks was independent of stimulus modality as well as stimulus type (i.e. target and non-target). This outcome supports also the previous finding that the target P3 elicited in the three-tone paradigm is essentially identical to the target P3 from a two-tone oddball or a single stimulus auditory paradigm (Polich et al., 1994; Katayama and Polich, 1996a; Mertens and Polich, 1997; Strüber and Polich, 2002; Wronka et al., 2007). The magnitude of late parietal P3 response to relevant target stimulus was found larger than in case of non-target tone in our study. This result is highly consistent with many reports using three-stimulus oddball paradigm (Polich, 1986; 1987; Katayama and Polich, 1996a; 1996b; 1999; Comerchero and Polich, 1999). However, contrary to some previous studies (Pfefferbaum et al., 1980) latency of parietal P3 deflection elicited by target tone was longer in comparison to the latency of non-target P3. This inconsistency could be partially explained by the fact that the relationship between latencies of target and non-target P3 was found to be modulated by the stimulus context. Particularly, Katayama and Polich (1998) manipulated the size of deviation between the standard and nonstandard auditory stimuli. They found that the larger is the size of physical difference between the frequent and rare tones, the longer is the latency of particular P3 deflection. Thus, when discrimination between standard and target stimuli become harder than differentiation between standard and non-target, then target P3 appear later than non-target P3 and *vice versa*. Similar results for auditory and visual modality were also reported by Comerchero and Polich (1999). Thus, it is reasonable to accept that component described here as the late parietal P3 is analogous to P3b in the literature.

Our manipulation of task instruction influenced also the magnitude of early frontal P3 response. The amplitude of this component in the active condition was found larger overall than in passive session. This result is in close agreement with previous studies (Katayama and Polich, 1999) were magnitude of frontal P3 response was suggested to be modulated by the strength of attentional focus. Specifically, a more difficult discrimination between targets and standards evokes a larger frontal P3 response to rare non-targets. These results demonstrate that voluntary attention could modulate the involuntary response to irrelevant but unexpected events. Similar effects were also reported for the visual modality (Comerchero and Polich, 1999) and auditory single stimulus task (Wronka et al., 2007). In addition, the latencies of early frontal P3 components measured in our passive condition were shorter than the latencies of equivalent peaks in active condition. The possible explanation for this effect is that larger

P3 response in active condition develops longer than the less pronounced deflection in passive condition.

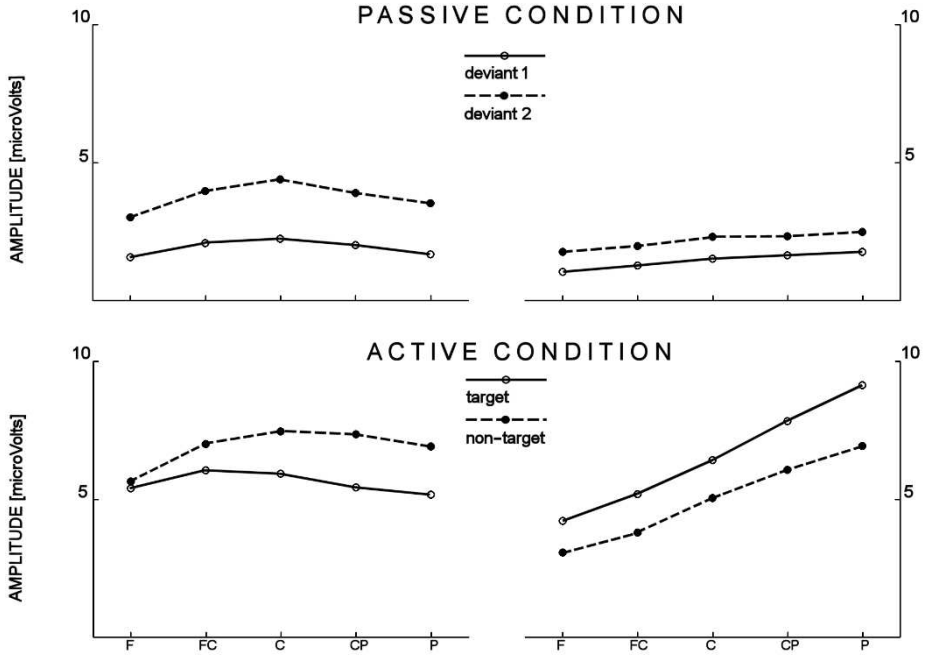


Fig. 10. Mean amplitudes of early P3 (left panel) and late P3 (right panel) from passive (deviant 1 and deviant 2 stimuli) and active (target and non-target stimuli) as a function of electrode locations. (F) frontal; (FC) fronto-central; (C) central; (CP) centro-parietal; (P) parietal.

The magnitude of early frontal P3 response was also consistently related to the size of stimulus deviation from standard. In the passive condition, the deviant 2 stimuli which is more different from the standard, elicited a larger P3 component than the equally probable deviant 1 stimuli. Similarly, in the active condition the P3 response to non-target stimuli was greater than the response to target stimuli of the same frequency. This effect is also compatible with the previous reports (Comerchero and Polich, 1999; Katayama and Polich, 1998; 1999). Moreover, it should be noticed that frontal P3 amplitude dependence on stimulus physical deviation was observed without any difference in probability of occurrence under both passive and active condition. This supports the thesis that stimulus

similarity or its discrimination difficulty importantly contribute to early frontal P3 generation (Comerchero and Polich, 1999).

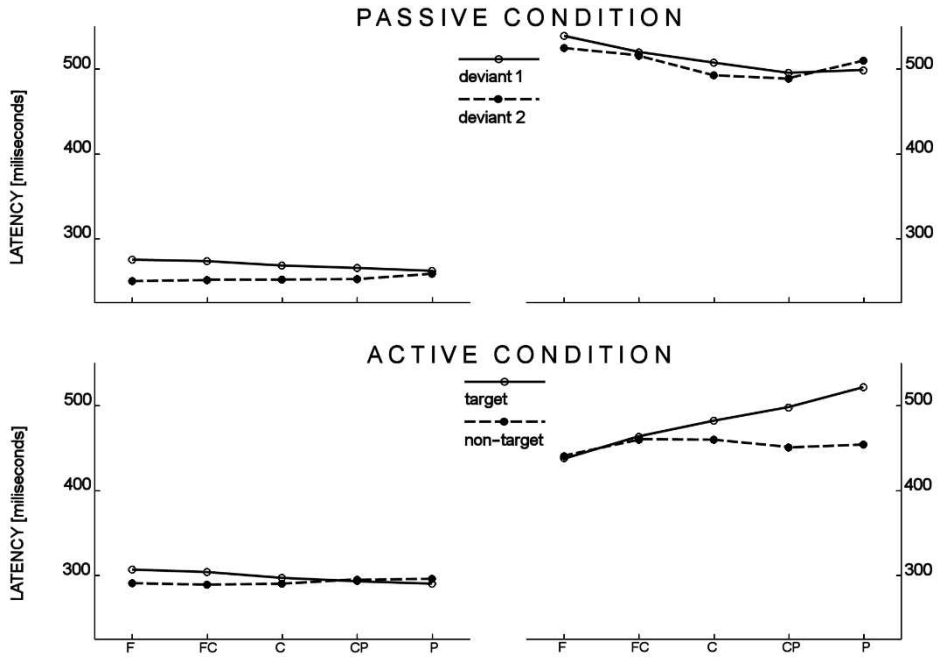


Fig. 11. Mean latencies of early P3 (left panel) and late P3 (right panel) from passive (deviant 1 and deviant 2 stimuli) and active (target and non-target stimuli) as a function of electrode locations. (F) frontal; (FC) fronto-central; (C) central; (CP) centro-parietal; (P) parietal.

At the same time, scalp distribution of frontal P3 component obtained in our experiment is consistent with reported in previous studies (Courchesne et al., 1975; Yamaguchi and Knight, 1991a; 1991b; Friedman and Simpson, 1994). Similar vertex maxima for this component were observed in case of both nonstandard stimuli in passive condition as well as for non-target tone in active condition. This could be interpreted as reflecting the activity of the same neuronal generator located within frontal lobe (Polich and Criado, 2006). However, maximum amplitude of P3 response elicited in our study by target stimulus in active condition was found slightly more anterior. The different scalp distribution of P3 response to target tone could be connected with the fact that for this type of events temporary representation in working memory was necessary. Single-cell recordings in animals and neuroimaging studies in human provide evidence that the

prefrontal cortex is important for working memory functions (D'Esposito et al., 2000; Passingham and Sakai, 2004). Thus, holding temporary representation of relevant event could therefore alter initial attention reallocation reflected by early frontal P3 component. This suggests that P3 neural generators were differentially engaged as a function of stimulus context demands. Accordingly, it seems acceptable to state that early frontal P3 component from our study is analogous to P3a in the literature.

## Conclusions

In conclusion, results of our experiment support the thesis that early frontal and late parietal P3 components of the ERP reflect two different sets of physiological and psychological processes. The frontal P3 could be related to early stages of initial attention engagement when distinct sensory information is gathered. Comparable basic characteristics of early frontal P3 responses measured in active and passive condition let us suggest that they reflected activity of very similar neural generator located within frontal cortex (Baudena et al., 1995). The characteristic of this activity depends on context within which perceptual changes reflecting unexpected event in environment take place. The larger the mismatch is between presented stimulus and passively formed neuronal trace, the more intense is the involuntary attentional switch toward the new event and the more pronounced is its electrophysiological correlate P3 component (Näätänen, 1990). In addition, this initial attention reallocation could be facilitated when subject voluntary direct their attention toward the ongoing perceptual events. The results obtained in our study also suggests that late parietal P3 generation is almost exclusively joint with the matching between the neuronal model of perceived stimulus and voluntarily maintained attentional trace of relevant event (Näätänen, 1990). The more advanced this process is, the greater is the P3 amplitude generated probably within posterior brain areas (Halgren et al., 1995a; 1995b). Although the neural loci for both early and late P3s generation are not yet completely clear there is growing body of evidence that interaction between frontal lobe and hippocampal/temporal-parietal areas are the most likely.

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# CHAPTER 4

## Neural generators of the auditory P3a and P3b *

**Abstract**

The aim of the present study was to define the scalp topography of the two subcomponents of the P3 elicited in a three-stimulus oddball paradigm and to identify their cortical generators using the standardized low resolution electromagnetic tomography (sLORETA). Subjects were presented with a random sequence of auditory stimuli and instructed to respond to an infrequently occurring target stimulus inserted into a sequence of frequent standard and rare non-target stimuli. Results show that the magnitude of the frontal P3a is determined by the relative physical difference among stimuli, as it was larger for the stimulus more deviant from the standard. Major neural generators of the P3a were localized within frontal cortex and anterior cingulate gyrus. In contrast to this, the P3b, showing maximal amplitude at parietal locations, was larger for stimuli demanding a response than for the rare non-target. Major sources of the P3b included the superior parietal lobule and the posterior part of the cingulate gyrus. Our findings are in line with the hypothesis that P3a is related to alerting activity during the initial allocation of attention, while P3b is related to activation of a posterior network when the neuronal model of perceived stimulation is compared with the attentional trace.

### Introduction

The P3 component of the event-related potentials is consistently related to attention, decision making, and memory updating and therefore provides a valuable tool for investigation of these processes in the human brain (see Polich and Criado, 2006; Polich, 2007; for a review). There is also strong evidence that this component represents the summation of activity from various widely distributed areas in the brain, and at least two subcomponents which temporally overlap can be distinguished, namely the P3a and the P3b (Polich and Criado, 2006). Each of these may reflect distinct information processing events.

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The P3a is a large positive deflection with a fronto-central distribution, and is typically elicited by novel or rare non-target stimuli inserted in a series of standard and target stimuli in the three-stimulus oddball paradigm. This component has relatively short peak latency (Courchesne et al., 1975; Friedman and Simpson, 1994). It was previously suggested that P3a reflects an alerting process in the frontal lobe when involuntary attention has to be redirected to unexpected events (Yamaguchi and Knight, 1991a). In contrast to this, the P3b (or classical P3) has a more posterior-parietal scalp distribution and a somewhat longer latency than P3a. There is broad evidence that this component can be regarded as reflecting target stimulus classification in tasks that require some form of action like a covert or overt response to stimuli (Donchin and Coles, 1988; Kok, 2001; Polich, 1998). Specifically, the P3b has been considered as indexing voluntary attention, such that its amplitude reflects the allocation of attentional resources (Kok, 2001; Wronka et al., 2007), and its peak latency is considered to be related to stimulus evaluation time (Kutas, McCarthy and Donchin, 1977).

Taken together, these two components appear to differ in their scalp distribution, magnitude, and peak latency as a function of the stimulus meaning. Therefore, it can be suggested that the P3a and P3b reflect distinct although strongly interrelated information processing events. Early P3a can be associated with the initial attention reallocation resulting from detection of the stimulus attribute change. This process follows original sensory processing and stimulus feature mismatch detection. Due to this, it has been previously suggested that the P3a is generally similar to the orienting response. Contrary to this, later P3b can be related to the voluntary stimulus classification. This process should engage working memory comparison, while the neuronal model of the stimulation is compared with the attentional trace of relevant information. It is reasonable to assume that the stimulus deviance detection initially engages attention (P3a) to facilitate the stimulus meaning assessment (P3b) which is associated with memory operations.

There is general agreement that both components stem from the activity of multiple neural generators. However, the exact location of these generators is still not precisely described. The frontal lobe is suggested as the source of the P3a. Patients with a frontal lesion demonstrate attenuated amplitude of the P3 recorded at frontal sites, while their parietal response can be less affected (Knight, 1984; Knight et al., 1995; Yamaguchi and Knight, 1991c). These data suggest that the dorsolateral prefrontal cortex makes a major contribution to the scalp recorded P3a. These results are in line with more recent neuroimaging and ERP studies demonstrating that activity of the frontal cortex can be related to detection of infrequent or alerting stimuli (McCarthy et al., 1997; Potts et al., 1996; Verbaten et al., 1997; see also Bocquillon et al., 2011 for review). A dipole analysis was also consistent with the notion of prefrontal involvement in novelty P3 generation (Mecklinger and Ullsperger, 1995). This is also consistent with Baudena et al. (1995),

where intracerebral potentials were measured in patients while they performed an auditory discrimination task with target and non-target rare stimuli. On the other hand, there is also evidence that activity within more posterior areas of the brain may play some role in the generation of the P3a component. Specifically, Halgren et al. (1995b) reported potentials recorded intracerebrally from patients as the responses to auditory and visual tasks, including the three-tone oddball paradigm, as well as the passive oddball task. They suggested that activity of the temporal pole, the middle temporal, the parahippocampal and the fusiform gyrus may be related to the non-specific orienting response that is also reflected in the scalp P3a. This is in line with reports from patients with focal hippocampal lesions, showing reduced amplitude of the P3a to novel distracters but a normal P3b component to targets (Knight, 1996). Decreased P3 response was also reported for patients with lesions located in the temporal-parietal junction (Yamaguchi and Knight, 1991c).

In contrast to this, there is a suggestion that neural generators of the P3b are located more posteriorly than the P3a. The more anterior located source for non-target P3 as compared to target P3 was recently reported by Barry and Rushby (2006) using LORETA source localization. This finding is consistent with results from human lesion research. Specifically, P3b amplitude is reduced after brain damage in the temporal-parietal junction (Knight et al., 1989; Yamaguchi and Knight, 1991b; Verleger et al., 1994), which suggests more posterior localization of its neural source when compared to P3a. This hypothesis could also be supported by the Halgren et al. (1995a) findings from intracerebral recording in patients. These authors reported that activity within superior temporal gyrus and hippocampus at about 380 ms post-stimulus may be reflected in the scalp P3b. This is also in line with recent magneto-encephalographic recording and functional imaging studies demonstrating that performing an oddball task activated several brain regions including the bilateral temporal-parietal cortex, thalamus, and anterior cingulate (Menon et al., 1997; Alho et al., 1998; Li, Wang and Hu, 2009; see also Bocquillon et al., 2011 for review). However, there is also evidence that dorsolateral prefrontal lesions can result in P3b reduction (Barcelo, Suwazono and Knight, 2000), which suggests that frontal cortex can be involved in generation of this component.

Taken together, it is reasonable to suggest that generation of the P3a and P3b stem from widespread activation within both frontal and parieto-temporal areas. Recent neuroimaging studies show that both target detection and distracter processing can be related to increased activation of frontal as well as parietal and temporal brain areas (Bledowski et al., 2004; Ebmeier et al., 1995; Kiehl et al., 2001; Kirino et al., 2000). It should be noticed that neuroimaging techniques provide relatively poor temporal resolution. Functional magnetic resonance imaging (fMRI) can provide maps of brain activation with millimeter spatial resolution however it is limited in its temporal precision

to the order of seconds. This technique enables to depict differences in brain activation elicited by distinct stimuli (e.g. targets, non-targets, standards in three-stimulus oddball task), but does not allow to define which of these differences are specifically related to the generation of the P3a or the P3b. It is reasonable to suppose that such distinction cannot be achieved in case of the hemodynamic response, which is typically delayed in onset after the neuronal activity and is prolonged in duration. For that reason, hemodynamic activity measured with fMRI in response to both targets and distracters can be rather associated with the indistinctive widespread activation underlying the whole P3 complex. Moreover, it cannot be completely excluded that the brain activation pattern observed in neuroimaging studies also reflects the generation of the ERP components other than the P3 (e.g. N2). Therefore, it is difficult to say whether results obtained with fMRI and the scalp-recorded positive ERP components dubbed as the P3a and P3b actually correspond to the same physiological processes. Hence, so far it is not clear to what extent frontal and parieto-temporal brain regions are involved in generation of P3a and P3b. Topographical analysis in a normal population suggests that the response to novel events activates the neural circuit that includes the prefrontal cortex and posterior regions of the brain (Friedman et al., 1993; Fabiani and Friedman, 1995). However, precise information about the role of these cortical regions in generation of the P3a and P3b is still lacking. This issue can be studied with the cortical source localization methods, which have been developed to link directly scalp-recorded ERP potentials with the cortical activity. It has recently been demonstrated that among such methods the Low Resolution Electromagnetic Tomography (LORETA) is the most promising for the source localization, especially when different cortical regions are expected to be simultaneously active (Yao and Dewald, 2005). Previous LORETA studies have reported neural sources of the P3 in the prefrontal cortex, the inferior and superior parietal cortex, the temporal lobe, and the cingulum (Anderer et al., 2003; Bocquillon et al., 2011; Barry and Rushby, 2006; Mulert et al., 2004; Wang et al., 2010; Volpe et al., 2007). Nevertheless, there has been, to our knowledge, no LORETA study where the activity elicited by targets and non-targets was compared separately in the P3a and P3b latency windows.

The main aim of the present study was to establish the neural generators of the P3a and P3b by recording ERPs in a three-tone oddball task and localizing the underlying activity using the Standardized Low Resolution Electromagnetic Tomography (sLORETA). The three-stimulus oddball paradigm is a modification of the oddball task in which rare non-target stimuli are inserted into a sequence of rare target and frequent standard stimuli. This procedure allows recording of clearly distinct P3a and P3b components (Wronka et al., 2008). Such distinction is not readily apparent when the traditional 2-stimulus oddball task is implemented (Polich, 1988). We expect that distinguishable P3a and P3b components would be measured in response to our target and non-target

auditory stimuli. However, due to the fact that participants were instructed to respond only to targets and to ignore non-targets, substantially different ERP waveforms would be elicited by each stimulus category. We predict that the early frontal P3a components measured in response to rare targets and non-targets would not differ significantly in their scalp topography. At the same time we expect the differences in their amplitudes, which can reflect different intensity of the early attention engagement, partially dependent on the physical properties of the stimulation. The greater the mismatch between the standard and rare stimuli, the stronger would be the attentional switch, and the larger would be the P3a response. Thus, we predict that non-target stimuli would elicit more evident P3a responses because the physical difference between our non-targets and standard was larger than the difference between targets and standards. Similarly, the parietal P3b responses elicited by target and non-target stimuli are not expected to differ in their scalp distribution, despite the expected differences in their amplitudes. Following many previous reports (Polich and Criado, 2006; Polich, 2007, for a review), we predict that P3b elicited by targets would exceed the response to non-targets. In order to determine clearly the P3 subcomponents, difference waves will be calculated by subtracting the standard stimulus ERP from ERPs elicited by targets and non-targets (Wronka et al., 2008). Neural generators of the P3a and P3b components will be separately established using the Standardized Low Resolution Electromagnetic Tomography (sLORETA). We will compare the LORETA images obtained for targets and non-targets with those computed for standard stimuli in order to determine brain regions showing differential activation during the P3a or P3b latency windows. We expect to observe activation of similar fronto-parietal network in response to targets and non-targets, which would correspond to the similarities in scalp distribution of the P3a and P3b elicited by targets and non-targets. Moreover, we will contrast the LORETA images obtained for targets and non-targets to reveal the differences in brain activation which can be associated with the expected differences in the amplitude of the P3a and P3b components. These brain areas can be therefore directly linked with the neural processes relevant for initial attention allocation and subsequent stimulus meaning evaluation.

## Methods

### Subjects

Twenty eight healthy students (24 women and 4 men; mean age = 21.2; S.D.=1.5 years) served as participants in the experiment. All of them were right-handed and had normal, or corrected to normal, vision, as well as normal hearing. They received course points for

their participation and signed an informed consent. All participants reported being free of neurological or psychiatric disorders, and absence of drug abuse and use of medication.

**Experimental procedure**

The EEG session lasted about twenty minutes. Subjects were seated in a darkened sound-isolated, air-conditioned chamber. They were asked to relax and to restrict body movements and blinking as much as possible while they were presented with a random series of tones (consisting of 1000Hz standard, 1100Hz target & 1200Hz non-target tones with probabilities of .8, .1 and .1 respectively). They were also asked to silently count the target tones and report the total number at the end of the session. Stimulus tones were presented with random ISI (1.25 s – 2 s) through a loudspeaker located in front of the subject at 65 dB SPL (100 ms duration with 10 ms rise/fall time).

**Electrophysiological recording**

The EEG was recorded using a BioSemi ActiveOne system with Ag–AgCl electrodes from 31 monopolar locations (Fp1, Fp2, F3, F4, F7, F8, FT7, FT8, FC3, FC4, T7, T8, C3, C4, TP7, TP8, CP3, CP4, P7, P8, P3, P4, O1, O2, AFz, Fz, FCz, Cz, CPz, Pz, Oz) according to the extended 10–20 system (Nuwer et al. 1998). Two additional electrodes (common mode sense (CMS) active electrode and driven right leg (DRL) passive electrode) were used as reference and ground electrodes, respectively; c.f. www.biosemi.com/faq/cms&drl.htm). All the cephalic electrodes were placed on the scalp using an Electro-Cap. The horizontal and vertical EOG were monitored by an additional 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. The EEG was acquired at a sampling rate of 512 Hz.

Output data were subsequently transferred to and stored in a computer for analysis. The EEG data were off-line re-referenced to an average montage, filtered with bandpass 0.016-30 Hz (24 dB), and sampled for 100 ms prior to stimulus onset and 900 ms after stimulus onset using BrainVision software. Finally, data were corrected for eye-movement artefacts (Gratton, Coles and Donchin, 1983). The ERP components of interest were defined as the largest positive going peaks within specific latency windows: 250-400 ms, and 400-700 ms for the P3a and P3b, respectively. These windows were selected on the basis of visual inspection of grand averaged ERPs obtained for each condition. Peak amplitude was calculated relative to the pre-stimulus baseline, and peak latency was measured from the time of stimulus onset.

Repeated-measures analyses of variance (ANOVA) were performed examining the effect of within-subjects factors of electrode LOCATION (5 anterior-to-posterior locations: Fz vs. FCz vs. Cz vs. CPz vs. Pz), and STIMULUS type (target vs. non-target) on P3 mean amplitudes. These electrodes were chosen due to the fact that P3 reaches its highest

amplitude at midline sites (Katayama and Polich, 1998; 1999). All analyses of variance employed Greenhouse-Geisser corrections to the degrees of freedom when appropriate, and only the corrected probability values are reported. The Bonferroni method was used for *post-hoc* comparisons, with a significance level of 0.05.

**Source localization – Standardized Low Resolution Electromagnetic Tomography (sLORETA)**

The sources of bioelectrical activity were estimated using the 2008 version of sLORETA (free academic software available at http://www.uzh.ch/keyinst/loreta.htm). The sLORETA images reflect the three-dimensional distribution of current density. The current implementation of sLORETA used the three-shell realistic head model (Fuchs et al., 2002) and electrode coordinates provided by Jurcak (Jurcak, Tzuzuki and Dan, 2007). All computations were made using the template from Montreal Neurological Institute MNI (Mazziotta et al., 2001), with the three-dimensional solution space restricted to cortical gray matter and hippocampus, as determined by the probabilistic Talairach atlas (Lancaster et al., 2000). The intracerebral volume is partitioned in 6239 voxels at 5 mm spatial resolution. The sLORETA images represent the standardized electric activity at each voxel in neuroanatomic MNI space as the exact magnitude of the estimated current density. Anatomical labels as Brodmann areas are also reported using MNI space, with correction to Talairach space (Brett, Johnsrude and Owen, 2002). The full description of the method can be found in (Pascual-Marqui, 2002). The proof of its exact, zero-error localization property is described in (Pascual-Marqui, 2007) and (Pascual-Marqui, 2009). The sLORETA images corresponding to P3a and P3b components were defined as the mean current density values for intervals between 250-400 ms post-stimuls and between 400-700 ms post-stimulus, respectively. Statistical significance of differences for sLORETA images elicited by the target and non-target stimuli was assessed with statistical nonparametric mapping tests for paired samples with correction for multiple comparisons, implemented in the version of sLORETA used (Nichols and Holmes, 2002).

## Results

**Event-related potentials**

The P3a amplitude obtained in response to target stimuli was significantly smaller than the P3a evoked by non-target stimuli. Maximal amplitudes of the P3a elicited by targets and non-targets were recorded at the vertex. This result is in close agreement with previous studies suggesting a link between activity of the frontal cortex and generation of the P3a component. The amplitude of the target P3b was significantly larger than the

P3b evoked by non-target stimuli. In both cases a typical topography with the maximum over parietal locations were observed. All these findings are confirmed by the statistical analyses presented in the next subsections. These effects are illustrated in figures 12 and 13.

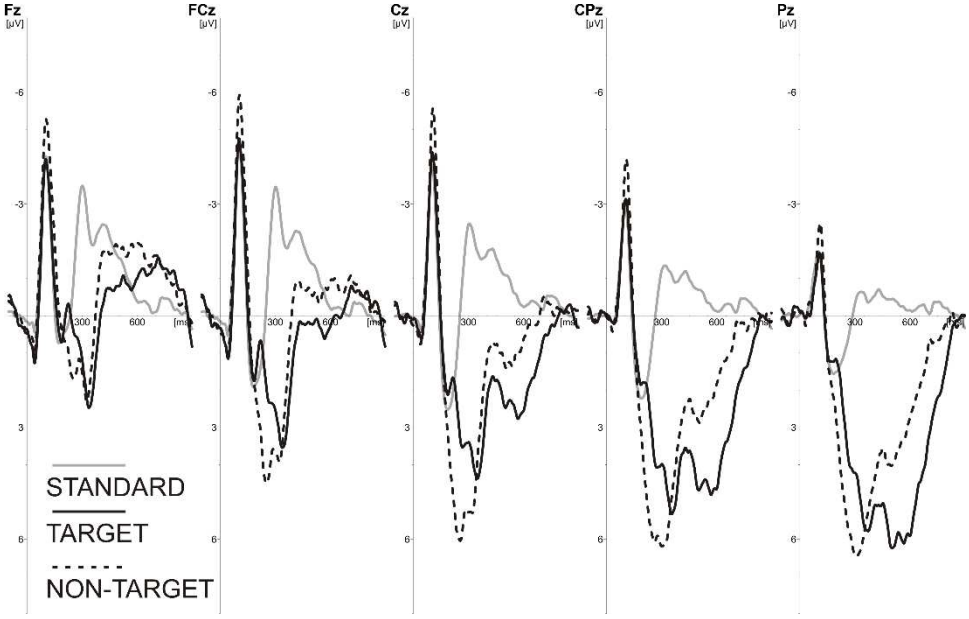


Figure 12. Grand averaged ERP responses to standard (grey line), target (solid black line), and non-target (dashed black line) stimuli recorded at 5 midline electrodes (Fz, FCz, Cz, CPz & Pz).

**Amplitude of P3a**

The amplitudes of the P3a component were initially assessed with a two-factor ANOVA (stimulus × location). Results obtained from the analysis suggest that a more pronounced P3a component was recorded in response to non-target stimuli when compared to targets, resulting in significant main effect of stimulus: $F(1,27)=7.53$, $P=.011$, when tested across 5 midline sites. Similarly, we found more pronounced non-target P3a response, as compared to target P3a, when analysis was restricted to vertex values: $F(1,27)=11.03$, $P=.003$. This difference is illustrated in Figures 12 and 13, which show ERP responses to target and non-target stimuli at midline electrodes. At the same time, a highly significant main effect of electrode location was also observed, $F(4,108)=17.71$, $P<.0001$, $\varepsilon=.431$. This effect suggests that P3a amplitude was substantially different over the 5 midline electrodes, which was confirmed by post-hoc comparisons. The lowest values were

obtained for the frontal Fz electrode, and a gradual increment was observed from the frontal location to the vertex, where the maximal P3a response was measured. Values obtained at parietal electrodes were lower in comparison to vertex but the difference did not reach significance. Similar topographies were observed for P3a elicited by target and non-target stimuli, which was confirmed by non-significant stimulus × location interaction, F(4,108)=1.31, P=.331, ε=.514. This effect is illustrated in figure 14, which shows the P3a distribution.

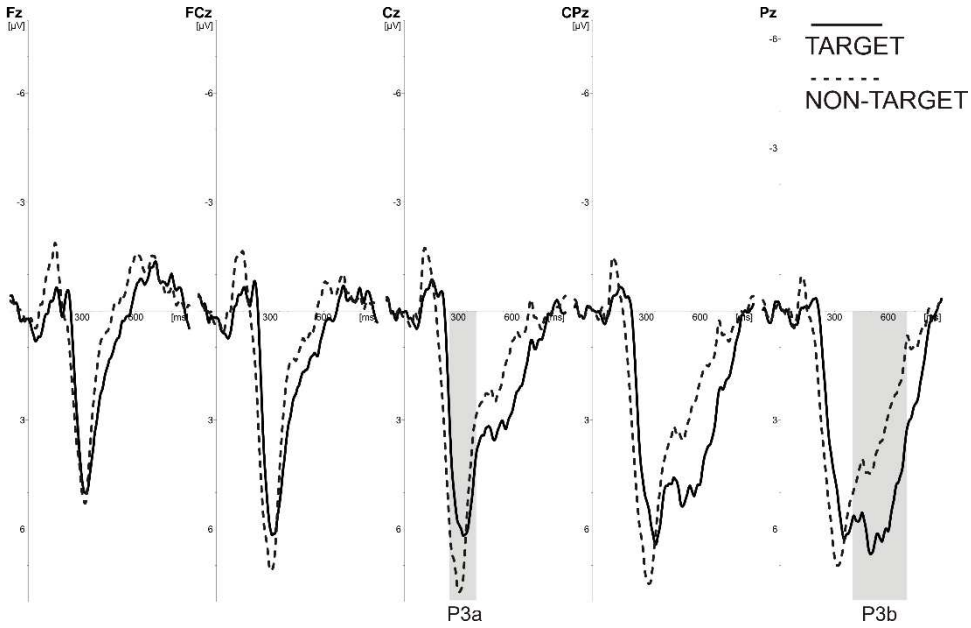


Figure 13. Grand averaged difference waveforms computed for target minus standard difference (solid black line) and non-target minus standard difference (dashed black line) at 5 midline electrodes (Fz, FCz, Cz, CPz & Pz).

**Amplitude of P3b**

A similar two-factor ANOVA (stimulus × location) was performed for the P3b amplitude. Obtained results show that higher P3b amplitude was recorded in response to target stimuli when compared to non-targets. However, this difference did not reach the level of significance [main effect of stimulus: F(1,27)=3.02, P=.094 when tested for 5 midline electrodes]. However, when amplitudes of P3b obtained at the parietal Pz electrode was analyzed, significantly higher values were obtained for target stimuli in comparison to non-targets: F(1,27)=27.44, P<.0001. Simultaneously, a highly significant main effect of

location was observed: F(4,108)=67.02, P<.0001, ε=.411. Topography of the P3b component in response to targets and non-targets is illustrated in figure 14. Amplitude of P3b elicited by targets and non-targets was found to be maximal at parietal locations and progressively increased from frontal to parietal regions. This effect was confirmed by post-hoc analysis. What should be also noticed, is the greater increase of P3b amplitude along the saggital plane for target in comparison to non-target stimuli, confirmed by a significant stimulus × location interaction: F(4,108)=7.72, P=.001, ε=.482.

**Source localization – Standardized Low Resolution Electromagnetic Tomography (sLORETA)**

**P3a component**

The rare targets and the rare non-targets produced widespread activation within the frontal, parietal, temporal and occipital brain areas between 250 and 400 ms after stimulus onset. Significantly increased bilateral activity of several brain areas was found in response to target stimuli when compared to standards. The most pronounced differences were found within the lateral frontal lobes (inferior, middle and superior frontal gyrus) as well as for the medial part of frontal cortex (the medial frontal gyrus and anterior cingulate gyrus). These brain regions appear to be the major neural sources of P3a component. A similar effect was also observed for the insula on both sides of the brain. Slightly smaller but still significant increases of brain activity elicited by targets was also recorded within left and right parietal lobes (inferior parietal lobule, angular gyrus, supramarginal gyrus, cingulate and posterior cingulate gyri), bilaterally within the temporal areas (superior, middle, inferior temporal gyri, and fusiform gyrus), as well as within the occipital cortex (superior, middle and inferior occipital gyri, cuneus). These effects are illustrated in the top left panel of Figure 14.

We obtained a similar pattern of results when the brain response to non-targets was contrasted with activity elicited by standard stimuli for the interval between 250 and 400 ms after stimulus onset. Again, significantly higher bilateral activation within the lateral (inferior, middle, and superior frontal gyrus) as well as the medial frontal cortex (medial frontal gyrus and anterior cingulate gyrus) was observed. Higher bilateral activations of the parietal lobes (inferior parietal lobule, angular gyrus, supramarginal gyrus, cingulate and posterior cingulate gyrus), the temporal areas (superior, middle, and inferior temporal gyrus, fusiform gyrus), and the occipital cortex (superior, middle and inferior occipital gyrus, cuneus) were observed in response to non-targets when contrasted to activity elicited by standard stimuli. These findings are illustrated in the bottom left panel of Figure 14.

| Comparison | Brain area | BA | MNI coordinates | | | t-score |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | |
| target vs standard | left CG | 24 | -5 | 0 | 30 | 5.12 |
| | right CG | 24 | 5 | 5 | 30 | 4.96 |
| P3a (250-400 ms) | left ACG | 24 | -10 | 20 | 25 | 5.06 |
| | right ACG | 32 | 5 | 45 | 10 | 4.97 |
| | left Ins | 13 | -35 | -5 | 20 | 5.07 |
| | right Ins | 45 | 30 | 25 | 5 | 4.52 |
| | left MFG | 6 | -25 | -10 | 45 | 5.02 |
| | right MFG | 11 | 35 | 60 | -10 | 4.93 |
| | left MeFG | 10 | -5 | 65 | 5 | 5.01 |
| | right MeFG | 10 | 5 | 65 | 5 | 5.00 |
| | left preCG | 6 | -35 | 0 | 30 | 5.02 |
| | right preCG | 4 | 20 | -25 | 55 | 4.37 |
| | left SFG | 10 | -5 | 60 | 0 | 4.99 |
| | right SFG | 10 | 5 | 60 | 0 | 4.99 |
| | left IFG | 9 | -35 | 5 | 30 | 4.97 |
| | right IFG | 11 | 10 | 40 | -20 | 4.78 |
| | left Reg | 11 | -5 | 55 | -25 | 4.83 |
| | right Reg | 11 | 5 | 55 | -25 | 4.85 |
| | left PCL | 31 | -5 | -15 | 50 | 4.85 |
| | right PCL | 31 | 5 | -15 | 50 | 4.71 |
| | left postCG | 3 | -35 | -25 | 40 | 4.81 |
| | right postCG | 5 | 5 | -45 | 65 | 4.34 |
| | left PCG | 23 | -5 | -30 | 25 | 4.76 |
| | right PCG | 23 | 5 | -30 | 25 | 4.57 |
| | left PHG | 34 | -20 | 0 | -15 | 4.64 |
| | right PHG | 34 | 15 | 0 | -15 | 4.23 |
| | left STG | 13 | -45 | -20 | 10 | 4.64 |
| | right STG | 38 | 30 | 20 | -30 | 4.24 |

Table 4. Brain regions showing significantly increased activation (at significance level P< 0.01) for target vs. standard comparison within the P3a latency window (250-400 ms poststimulus). Abbreviations: ACG anterior cingulate gyrus; CG cingulate gyrus; PCG posterior cingulate gyrus; preCG precentral gyrus; postCG postcentral gyrus; Ins insula; IFG inferior frontal gyrus; MeFG medial frontal gyrus; MFG middle frontal gyrus; SFG superior frontal gyrus; Reg rectal gyrus; PHG parahippocampal gyrus; PCL paracentral lobule; SPL superior parietal lobule; STG superior temporal gyrus; preCU precuneus

| Comparison | Brain area | BA | MNI coordinates | | | t-score |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | |
| non-target vs standard | left CG | 31 | -5 | -30 | 45 | 4.62 |
| | right CG | 24 | 5 | -20 | 45 | 4.57 |
| P3a (250-400 ms) | left ACG | 33 | -5 | 10 | 25 | 4.53 |
| | right ACG | 32 | 5 | 40 | 20 | 4.56 |
| | left Ins | 13 | -35 | -5 | 20 | 4.24 |
| | right Ins | 13 | 30 | 20 | 15 | 3.91 |
| | left MFG | 6 | -20 | -15 | 65 | 4.45 |
| | right MFG | 10 | 20 | 60 | 25 | 4.49 |
| | left MeFG | 6 | -10 | -30 | 55 | 4.64 |
| | right MeFG | 10 | 5 | 65 | 20 | 4.59 |
| | left preCG | 4 | -15 | -35 | 60 | 4.63 |
| | right preCG | 4 | 10 | -30 | 70 | 4.41 |
| | left SFG | 10 | -5 | 60 | 0 | 4.47 |
| | right SFG | 9 | 10 | 50 | 25 | 4.55 |
| | left IFG | 47 | -20 | 30 | -5 | 4.17 |
| | right IFG | 10 | 40 | 55 | 5 | 4.09 |
| | left Reg | 11 | -5 | 55 | -25 | 4.16 |
| | right Reg | 11 | 5 | 55 | -25 | 4.15 |
| | left PCL | 5 | -10 | -40 | 55 | 4.64 |
| | right PCL | 6 | 5 | -30 | 50 | 4.58 |
| | left postCG | 4 | -10 | -40 | 60 | 4.62 |
| | right postCG | 5 | 5 | -45 | 65 | 4.47 |
| | left PCG | 23 | -5 | -30 | 25 | 4.36 |
| | right PCG | 23 | 5 | -30 | 25 | 4.27 |
| | left PHG | 28 | -25 | -20 | -10 | 3.92 |
| | right PHG | 34 | 15 | 0 | -15 | 3.54 |
| | left SPL | 5 | -20 | -45 | 60 | 4.58 |
| | right SPL | 5 | 20 | -45 | 65 | 4.37 |
| | left preCU | 7 | -5 | -35 | 45 | 4.61 |
| | right preCU | 7 | 5 | -35 | 45 | 4.55 |

Table 5. Brain regions showing significantly increased activation (at significance level P< 0.01) for non-target vs. standard comparison within the P3a latency window (250-400 ms poststimulus). Abbreviations: ACG anterior cingulate gyrus; CG cingulate gyrus; PCG posterior cingulate gyrus; preCG precentral gyrus; postCG postcentral gyrus; Ins insula; IFG inferior frontal gyrus; MeFG medial frontal gyrus; MFG middle frontal gyrus; SFG superior frontal gyrus; Reg rectal gyrus; PHG parahippocampal gyrus; PCL paracentral lobule; SPL superior parietal lobule; STG superior temporal gyrus; preCU precuneus

These results suggest that the overall pattern of activity measured within the P3a latency window is highly similar for target and non-target stimuli. Hence, we compared sLORETA images obtained for the targets and non-targets to localize the brain regions differently activated by these stimuli. Direct comparison of the sLORETA current source density maps

acquired for P3a interval revealed several brain areas where higher activation was observed bilaterally in response to non-targets compared to targets. Specifically, we found increased activity within the frontal region (inferior, middle, and superior frontal gyri, anterior cingulate and cingulate gyri, as well as medial frontal gyrus) and within temporal areas (parahippocampal gyrus and uncus). We also found significantly greater activation of the orbital gyrus and insula, but only in the right hemisphere. Other areas in which significant differences were found are summarized in Table 8 and illustrated in the left panel of Figure 15.

**P3b component**

The widespread bilateral activation of frontal, parietal, temporal and occipital brain areas were also observed when sLORETA images obtained for the interval between 400 and 700 ms after stimulus onset in response to rare targets and rare non-targets were compared to those elicited by frequent standard stimuli. Specifically, exposition of the target stimuli leads to most evident increase of activation within the parietal lobes (superior parietal lobule, inferior parietal lobule, postcentral gyrus, posterior cingulate gyrus). This finding suggests that these brain areas are major neural sources of the P3b component. A similar bilateral effect was obtained for the lateral frontal areas (inferior, middle and superior frontal gyrus) as well as for the medial part of the frontal cortex (medial frontal gyrus and anterior cingulate gyrus). This effect was also observed for the insula on the both side of the brain. Slightly smaller but still significant effect was also recorded bilaterally for the temporal areas (superior temporal gyrus), as well as in case of the occipital cortex (fusiform gyrus, cuneus). These effects are illustrated in the top right panel of Figure 14.
Similar pattern of results within the same latency interval (400-700 ms post-stimulus) were obtained when brain responses to non-targets were compared to activity elicited by standard stimuli. We observed significantly higher bilateral activation within the parietal (superior parietal lobule, posterior cingulate gyrus) and frontal cortex (superior frontal gyrus, middle frontal gyrus, inferior frontal gyrus, medial frontal gyrus and anterior cingulate gyrus). More pronounced activation of the temporal areas (superior temporal gyrus) was also observed in response to non-targets c.f. standard stimuli. These findings are illustrated in the bottom right panel of Figure 14.

| Comparison | Brain area | BA | MNI coordinates | | | t-score |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | |
| target vs standard | left CG | 24 | -5 | -10 | 50 | 9.62 |
| | right CG | 24 | 5 | -10 | 50 | 9.38 |
| P3b (400-700 ms) | left ACG | 33 | -5 | 10 | 25 | 7.55 |
| | right ACG | 24 | 10 | 20 | 30 | 7.23 |
| | left Ins | 13 | -35 | -20 | 20 | 7.26 |
| | right Ins | 13 | 30 | 15 | 15 | 4.84 |
| | left MFG | 6 | -20 | -15 | 65 | 9.49 |
| | right MFG | 6 | 20 | -10 | 65 | 8.60 |
| | left MeFG | 6 | -10 | -25 | 55 | 9.90 |
| | right MeFG | 6 | 5 | -20 | 60 | 9.60 |
| | left preCG | 4 | -15 | -30 | 60 | 9.90 |
| | right preCG | 6 | 10 | -20 | 70 | 9.32 |
| | left SFG | 6 | -15 | -15 | 70 | 9.48 |
| | right SFG | 6 | 5 | -10 | 70 | 9.15 |
| | left IFG | 9 | -35 | 5 | 30 | 6.42 |
| | right IFG | 10 | 40 | 55 | 5 | 5.05 |
| | left PCL | 31 | -10 | -15 | 50 | 9.75 |
| | right PCL | 31 | 5 | -15 | 50 | 9.39 |
| | left postCG | 3 | -20 | -30 | 60 | 9.80 |
| | right postCG | 4 | 10 | -35 | 70 | 8.97 |
| | left PCG | 23 | -5 | -30 | 25 | 7.46 |
| | right PCG | 23 | 5 | -30 | 25 | 6.97 |
| | left preCU | 7 | -5 | -35 | 45 | 8.97 |
| | right preCU | 7 | 5 | -35 | 45 | 8.49 |
| | left SPL | 5 | -20 | -45 | 65 | 9.24 |
| | right SPL | 5 | 20 | -45 | 65 | 7.91 |
| | left IPL | 40 | -35 | -35 | 45 | 8.11 |
| | right IPL | 40 | 35 | -45 | 55 | 5.81 |

Table 6. Brain regions showing significantly increased activation (at significance level P< 0.05) for target vs. standard comparison within the P3b latency window (400-700 ms poststimulus). Abbreviations: ACG anterior cingulate gyrus; CG cingulate gyrus; PCG posterior cingulate gyrus; preCG precentral gyrus; postCG postcentral gyrus; Ins insula; IFG inferior frontal gyrus; MeFG medial frontal gyrus; MFG middle frontal gyrus; SFG superior frontal gyrus; PCL paracentral lobule; SPL superior parietal lobule; IPL inferior parietal lobule; preCU precuneus

| Comparison | Brain area | BA | MNI coordinates | | | t-score |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | |
| non-target vs standard P3b (400-700 ms) | left CG | 24 | -5 | -20 | 40 | 6.74 |
| | right CG | 24 | 5 | -15 | 40 | 6.74 |
| | left ACG | 33 | -5 | 10 | 25 | 6.07 |
| | right ACG | 33 | 5 | 10 | 25 | 6.32 |
| | left Ins | 13 | -30 | -30 | 20 | 5.22 |
| | right Ins | 13 | 30 | 15 | 15 | 4.71 |
| | left MFG | 6 | -20 | -15 | 65 | 5.98 |
| | right MFG | 6 | 25 | -10 | 45 | 5.93 |
| | left MeFG | 6 | -10 | -25 | 50 | 6.66 |
| | right MeFG | 6 | 5 | -20 | 55 | 6.54 |
| | left preCG | 4 | -15 | -30 | 60 | 6.46 |
| | right preCG | 4 | 20 | -25 | 55 | 6.06 |
| | left SFG | 6 | -5 | 5 | 55 | 5.94 |
| | right SFG | 6 | 5 | 5 | 55 | 6.10 |
| | left IFG | 9 | -35 | 5 | 30 | 4.26 |
| | right IFG | 9 | 35 | 5 | 30 | 4.91 |
| | left PCL | 31 | -5 | -25 | 45 | 6.72 |
| | right PCL | 31 | 5 | -20 | 50 | 6.64 |
| | left postCG | 3 | -20 | -30 | 50 | 6.45 |
| | right postCG | 4 | 10 | -40 | 65 | 5.94 |
| | left PCG | 23 | -5 | -30 | 25 | 6.05 |
| | right PCG | 23 | 5 | -30 | 25 | 5.87 |
| | left preCU | 7 | -5 | -35 | 45 | 6.47 |
| | right preCU | 7 | 5 | -35 | 45 | 6.30 |
| | left SPL | 5 | -20 | -45 | 60 | 6.06 |
| | right SPL | 5 | 20 | -45 | 65 | 5.37 |

Table 7. Brain regions showing significantly increased activation (at significance level P< 0.05) for non-target vs. standard comparison within the P3b latency window (400-700 ms poststimulus). Abbreviations: ACG anterior cingulate gyrus; CG cingulate gyrus; PCG posterior cingulate gyrus; preCG precentral gyrus; postCG postcentral gyrus; Ins insula; IFG inferior frontal gyrus; MeFG medial frontal gyrus; MFG middle frontal gyrus; SFG superior frontal gyrus; PCL paracentral lobule; SPL superior parietal lobule; IPL inferior parietal lobule; preCU precuneus

Obtained results let us suggest that the overall pattern of activity measured within the P3b latency window is comparable for target and non-target stimuli. Therefore, we compared sLORETA images obtained for the targets and non-targets to localize the brain regions differently activated by these stimuli. Direct comparison of the sLORETA current source density maps acquired for the P3b interval revealed several brain areas where higher activation was observed bilaterally in response to targets when compared to non-targets. Specifically, we found increased activity within the parietal region (superior parietal lobule, inferior parietal lobule, paracentral lobule, postcentral gyrus, posterior cingulate gyrus) and within frontal areas (superior frontal gyrus, medial frontal gyrus).

Additionally, we also found significantly greater activation of the precuneus and cuneus. Other areas, in which significant differences were found, are summarized in Table 8 and illustrated in the right panel of Figure 15.

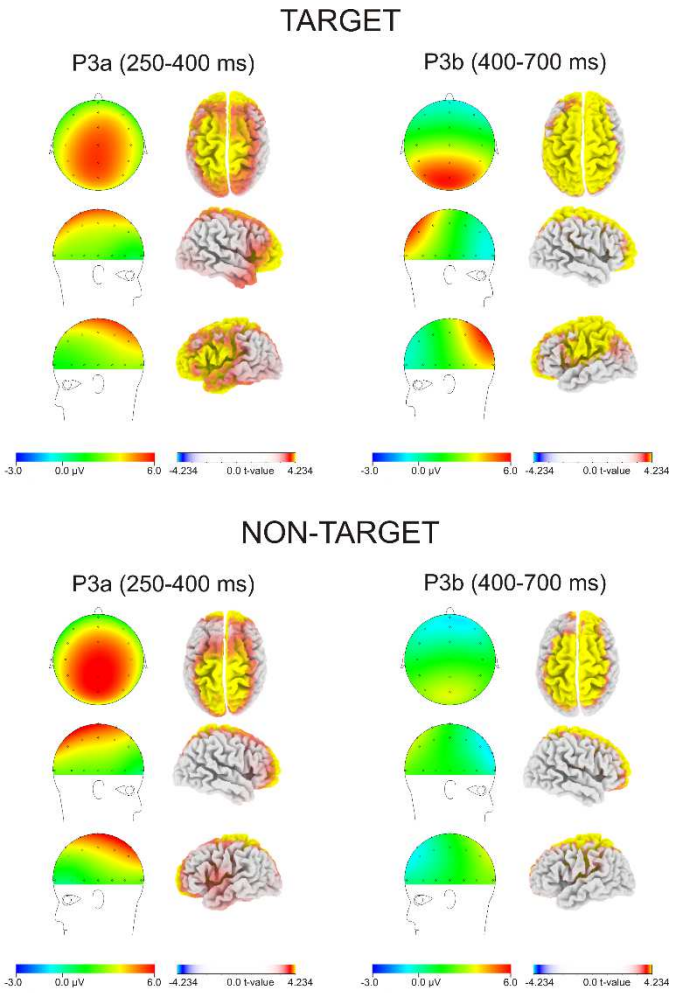


Figure 14. ERP topographical maps showing voltage differences and corresponding sLORETA three dimensional maps of voxel-by-voxel *t*-statistics representing target minus standard difference (upper panel) and non-target minus standard difference (lower panel). The sLORETA scales show negative (blue) and positive (red) *t*-values for which the alpha is significant after Holmes' correction for multiple comparisons.

| Comparison | Brain area | BA | MNI coordinates | | | t-score |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | |
| target vs non-target P3a (250-400 ms) | right MeFG | 6 | 10 | 0 | 65 | -3.36 |
| | left MeFG | 6 | -5 | -5 | 65 | -3.27 |
| | right SFG | 6 | 10 | -5 | 70 | -3.35 |
| | left SFG | 6 | -5 | 0 | 70 | -3.26 |
| | right CG | 24 | 5 | -5 | 50 | -3.33 |
| | left CG | 24 | -5 | -5 | 50 | -3.25 |
| | right MFG | 6 | 15 | 5 | 65 | -3.30 |
| | left MFG | 6 | -15 | -10 | 65 | -3.10 |
| | right PCL | 31 | 5 | -15 | 50 | -3.25 |
| | left PCL | 31 | -5 | -15 | 50 | -3.19 |
| | right ACG | 25 | 5 | 5 | -5 | -3.17 |
| | left ACG | 25 | -5 | 15 | -10 | -3.08 |
| | right preCG | 6 | 10 | -20 | 70 | -3.14 |
| | left preCG | 6 | -10 | -20 | 70 | -3.03 |
| | right PHG | 34 | 15 | 0 | -15 | -3.01 |
| | left PHG | 28 | -15 | -5 | -15 | -3.02 |
| | right Reg | 11 | 5 | 15 | -20 | -3,00 |
| | right Ins | 13 | 30 | 15 | 15 | -2.97 |
| | right IFG | 47 | 15 | 20 | -15 | -2.94 |
| | left IFG | 47 | -15 | 20 | -15 | -2.85 |
| | right PCG | 23 | 5 | -30 | 25 | -2.94 |
| | left PCG | 23 | -5 | -30 | 25 | -2.92 |
| target vs non-target P3b (400-700 ms) | right SPL | 5 | 20 | -45 | 60 | 4.18 |
| | left SPL | 5 | -20 | -45 | 60 | 3.86 |
| | right PCL | 4 | 5 | -40 | 70 | 4.17 |
| | left PCL | 4 | -5 | -40 | 60 | 4.15 |
| | right postCG | 4 | 10 | -35 | 70 | 4.16 |
| | left postCG | 4 | -10 | -40 | 60 | 4.10 |
| | right preCG | 4 | 35 | -25 | 65 | 3.19 |
| | left preCG | 4 | -35 | -20 | 45 | 3.11 |
| | right SFG | 6 | 20 | -10 | 70 | 3.16 |
| | left SFG | 6 | -20 | -5 | 70 | 3.11 |
| | right IPL | 40 | 30 | -60 | 45 | 3.10 |
| | left IPL | 40 | -35 | -35 | 45 | 3.14 |
| | right PCG | 31 | 5 | -55 | 30 | 3.13 |
| | right MeFG | 6 | 5 | -5 | 60 | 3.09 |
| | left MeFG | 6 | -5 | -5 | 65 | 3.11 |
| | right preCU | 31 | 10 | -55 | 30 | 3.09 |
| | left preCU | 19 | -15 | -85 | 40 | 3.11 |
| | right CG | 31 | 5 | -60 | 30 | 3.10 |
| | left CG | 31 | -5 | -40 | 30 | 3.11 |

Table 8. Brain regions showing significantly decreased activation (at significance level $P < 0.05$) for target vs. non-target comparison within the P3a latency window (250-400 ms poststimulus) and significantly increased activation (at significance level $P < 0.05$) for target vs. non-target comparison within the P3b latency window (400-700 ms poststimulus).

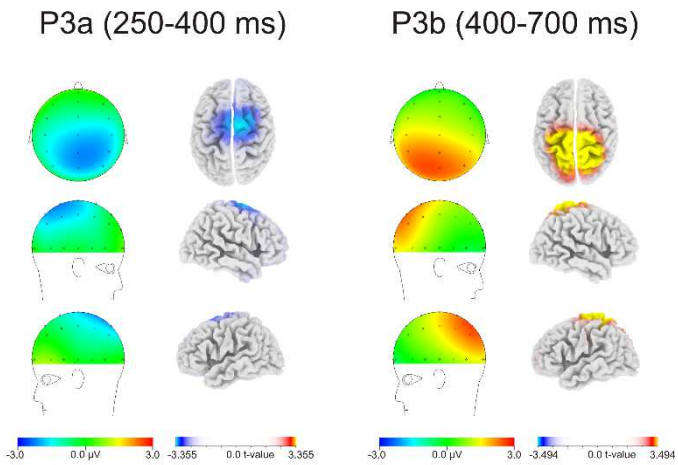


Figure 15. ERP topographical maps showing voltage differences and corresponding sLORETA three dimensional maps of voxel-by-voxel *t*-statistics representing target minus non-target difference, corresponding to the P3a (left panel) and the P3b (right panel) latency windows. The sLORETA scales show negative (blue) and positive (red) *t*-values for which the alpha is significant after Holmes' correction for multiple comparisons.

## Discussion

The main aim of the present study was to establish the neural generators of the P3a and P3b by recording ERPs in a three-stimulus oddball task which previously has been successfully used to elicit these components separately (Wronka et al., 2008). The results of our study confirmed recent findings that the P3 complex obtained in response to rare targets and rare non-targets can be differentiated according to its amplitudes measured over frontal-central and parietal sites (Comerchero and Polich, 1999; Katayama and Polich, 1999). Specifically, when our experimental instruction demanded to attention resources be allocated to discrimination of auditory stimuli, evident P3 deflections were obtained for both target and non-target stimuli. In both cases, the P3 complex was divided into early P3a and late P3b components by subtracting ERPs elicited by standard tones from ERPs recorded in response to the targets or non-targets. The amplitude of the early frontal P3a was found to be larger when elicited by non-targets than targets. It is important to note that the frequency difference between the non-target stimulus and the frequent standards was twice the difference between targets and standards. This effect extends previous findings suggesting a relationship between stimulus deviance and the

magnitude of the P3a response (Wronka et al., 2008). Generally, the larger is the mismatch between physical characteristics of the presented stimulus and the passively formed neuronal trace, the more intense is the initial attention engagement reflected in the P3a component (Näätänen, 1990).

In contrast to this, amplitude of the P3b recorded at parietal sites to targets was larger than to non-targets. This result is consistent with many previous reports (Polich and Criado, 2006; Polich 2007, for a review), suggesting that P3b component can be related to the process of voluntary stimulus evaluation which is based on matching between the neuronal model of perceived stimulus and the previously formed attentional template of the relevant event. Our results are also in line with the suggestion that the neural generator of the P3b can be located mainly within the parietal and temporal cortices. Maximal amplitudes of this component elicited by target and non-target were obtained over parietal sites.

LORETA results obtained in our study indicated that the P3a component of the ERP can be related to increased activity within a widely distributed brain network, located predominantly within the frontal cortex. Activation of additional brain areas located within the parietal, temporal and occipital regions was also found for the P3a latency window. A highly similar pattern of effects was obtained for the target stimuli as well as for the non-targets, which is in line with the results from analysis of the ERP data, showing comparable topography of this component elicited by targets and non-targets. What is important in this context is our finding that activity within dorsolateral and medial parts of the frontal lobes can be directly linked to differences in scalp recorded P3a. Specifically, amplitude of P3a was greater in response to non-targets than targets in our study. At the same time, activity of the medial part of the frontal lobes was higher for the non-targets than targets. This finding indicates that the frontal cortex plays an important role in generating the P3a component. Therefore, it is reasonable to suggest that the activity in the dorsolateral and medial frontal areas can be directly related to initial attention reallocation following detection of stimulus change.

These findings correspond closely to previous reports from neuroimaging studies where distracter processing was linked with increased activation of both frontal and parietal brain areas (Bledowski et al., 2004; Ebmeier et al., 1995; Kiehl et al., 2001; Kirino et al., 2000). Similarly, recent source localization studies also report neural origin of the P3 in the same set of brain areas (Anderer et al., 2003; Bocquillon et al., 2011; Barry and Rushby, 2006; Mulert et al., 2004; Wang et al., 2010; Volpe et al. 2007). This is also consistent with the previously reported effect of P3a diminishment as the result of frontal lobe lesions (Knight, 1984). Our results are also in line with data reported from studies where intracerebral potentials elicited in an auditory oddball paradigm were measured in patients (Baudena et al., 1995).

Results obtained in this study indicate also that major sources of the P3b component can be located more posterior in comparison to the P3a, which is consistent with recent LORETA studies (Barry and Rushby, 2006; Volpe et al., 2007). We found that the scalp recorded P3b component can be related to enhanced activity of a broad neural network including frontal, parietal and temporal cortical regions. It should be also noted that much larger activation was observed in response to targets than to non-targets. This effect closely corresponds to differences obtained in scalp recorded EEG in our study where amplitude of the target P3b was larger than the non-target P3b. These findings are in line with previous reports where P3b to stimuli demanding overt or covert response was consistently larger than to both standard and distracter stimuli (Polich and Criado, 2006). Enhanced activation of similar structures was also reported in neuroimaging studies (Bledowski et al., 2004; Ebmeier et al., 1995; Kiehl et al., 2001; Kirino et al., 2000).

Taken together, our results suggest that both P3a and P3b stem from activation of broad neuronal networks located within the frontal, parietal and temporal lobes. This network is activated when distinctive change in the environment takes place, resulting in initial attention engagement. The more salient is the stimulus, the more intense is this bottom-up process, and the more pronounced is its electrophysiological correlate – the P3a component. The larger is the mismatch, between the presentation of the actual stimulus and the neuronal trace related to previously perceived stimuli, the greater is the involuntary attention switch. In contrast to this, activity linked with P3b generation can be rather related to the later phase of information processing, when the neuronal model of the perceived stimulus is confronted with the voluntarily maintained attentional trace of the relevant event (Näätänen, 1990). The more advanced this process is, the greater is the P3b amplitude.

It was recently suggested that generation of the P3a and the P3b components can be linked with the phasic activation of the neuromodulatory locus coeruleus–norepinephrine (LC-NE) system (see Nieuwenhuis et al., 2005, for details). It is important to note that the conditions when specific phasic activity of LC-NE system can be observed closely correspond to conditions under which P3 responses are measured. Specifically, LC activity in monkey have been investigated in the visual oddball task and it was found that LC neurons were phasically activated selectively by presentation of the target stimuli and only weakly or not at all by presentation of non-target stimuli. Moreover, amplitude of the LC neurons' phasic response to targets was affected by probability in a way similar to the P3. Novel stimuli typically elicit an LC phasic response and this response habituates quickly with repeated presentations. It should also be noted that there is evidence suggesting that brain regions innervated by NE are broadly consistent with areas involved in P3 generation. Moreover, the latency differences between the frontal P3a and the more posterior P3b might be explained by the anatomy of noradrenergic fibers, which

first innervate the frontal cortex and then continue caudally to more posterior cortical areas. Other neuromodulatory systems can also play an important role in P3 generation and therefore should be investigated more thoroughly. Specifically, available evidence suggests that P3a is related to frontal attention system mediated by dopaminergic activity. Parkinson disease patients who demonstrate decreased level of dopamine show also deficient P3 measures. Results from pharmacological studies have suggested that dopamine level is related to amplitude and latency of P3 (see Polich and Criado, 2006 for details).

## Conclusions

In conclusion, our results support the hypothesis that frontal P3a and parietal P3b components of the ERP reflect two different processes within human brain. Frontal P3a can be linked with the initial allocation of attention. The topography of this component as well as source localization data obtained in this study suggest that neural sources of P3a are located within the frontal lobe and anterior cingulate cortex. Our results also suggest that parietal P3b can be connected to the effortful evaluation of stimulus meaning. Thus, P3b is generated when the neuronal model of the stimulus is compared to the voluntarily maintained attentional trace of a relevant event. Major neural sources of the P3b were found within parietal lobe and posterior cingulate cortex. Our results are in line with the suggestion that both processes engage widespread networks of frontal and temporal-parietal cortical areas.

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# CHAPTER 5

## Psychometric intelligence and P3 of the event-related potentials studied with a 3-stimulus auditory oddball task *


**Abstract**

Relationship between psychometric intelligence measured with Raven's Advanced Progressive Matrices (RAPM) and event-related potentials (ERP) was examined using 3-stimulus oddball task. Subjects who had scored higher on RAPM exhibited larger amplitude of P3a component. Additional analysis using the Standardized Low Resolution Electromagnetic Tomography (sLORETA) revealed that this effect corresponds with stronger activity within the frontal cortex and the cingulate gyrus. High intelligence can also be linked with greater P3b response and stronger activity within the parietal cortex and the posterior cingulate gyrus. It may be concluded that the processes related to the initial stage of attention engagement as indexed by P3a, as well as the later stimulus evaluation and classification reflected in P3b, are more intense in subjects scoring higher on RAPM. The quality of mental abilities can therefore be related to differences of the activity in frontal and parietal brain regions.


### Introduction

Event-related potentials (ERPs) with their high temporal resolution provide important information about neural activity related to mental activity. Aspects of information processing which are closely linked to attentional resource allocation, can be studied through measurement of P3 (or P300), a frequently investigated endogenous ERP component. It is a positive potential, most easily recorded in the 'oddball task', peaking between 250 and 600 ms and maximal at centro-parietal areas (Polich and Criado, 2006; Polich, 2007). P3 reflects cognitive processing, such as stimulus identification and elaboration while the amplitude is thought to reflect resource allocation of attention (Donchin and Coles, 1988; Kok, 2001; Polich, 1998; Verleger, 1988). The amplitude and


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latency of this component can be used as marker of the intensity and timing of cognitive processes.

The latency of P3 seems to be negatively correlated with the level of intelligence (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Egan et al., 1992; McGarry-Roberts, Stelmack and Campbell, 1992; Polich and Martin, 1992; Zurron and Diaz, 1998). This might be interpreted as an indication that intelligence is inversely related to the speed of processing. At the same time, however, the relationship between P3 amplitude and intelligence is far from clear. Amplitude of P3 has been found to be negatively correlated with intelligence a study of McGarry-Roberts et al. (1992) and Zhang, Caryl and Deary (1989). On the other hand, in several other studies a positive correlation between amplitude of P3 and intelligence has been reported (Alcorn and Morris, 1996; Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008). Even, in some cases a near zero correlation between P3 amplitude and intelligence is reported (Houlihan, Stelmack and Campbell, 1998).

This contradiction results may be partially explained by major differences in research procedures. For example, a negative correlation can result from studies in which subjects are tested for their memory, while positive relations could be obtained when primary perceptual tasks are used implementing detection of stimuli. Thus, in each case two different sets of cognitive processes are initiated, and simultaneously two different sets of ERP components are measured. The P3 measured in memory tasks could overlap with the 'slow wave', a negative deflection appearing in a similar time window as the P3 and related to memory rehearsal (Kok, 2001). The temporal summation of P3 and slow wave could lead to an attenuation of the P3 amplitude (Kok, 1997). A negative correlation between intelligence and P3 amplitude measured in memory tasks could indicates differences in the intensity of memory recall. The more intense the memory processing, the greater the reduction of the P3 amplitude is. On the other hand, when P3 is measured in perceptual tasks, no such overlap is expected, and a positive correlation between intelligence and P3 amplitude can be obtained.

It is important to notice that P3 is not a unitary potential but that it rather represents the summation of activities from widely distributed brain areas, reflecting distinct information processing stages. A distinction can be made between two subcomponents which temporally overlap named P3a and P3b (Polich and Criado, 2006; Polich, 2007; Wronka, Kaiser and Coenen, 2008). P3a has a fronto-central distribution, with a relatively short peak latency, reflecting involuntary engagement of attention during processing of novel and salient stimuli (Yamaguchi and Knight, 1991). This component is typically recorded in a three-stimulus oddball paradigm (Comerchero and Polich, 1999; Katayama and Polich, 1999; Wronka, Kaiser and Coenen, 2008), and is not readily apparent in a

traditional two-stimulus oddball task (Polich, 1998). P3b (or classical P3) has a more posterior-parietal distribution, longer latency, reflecting target stimulus classification when a response to stimuli is required (Donchin and Coles, 1988; Kok, 2001). Specifically, the P3b amplitude indexes voluntary allocation of attentional resources (Kok, 2001; Wronka et al., 2007), while latency can be related to stimulus evaluation time (Kutas, McCarthy and Donchin, 1977). Due to this distinction it can be suggested that the relationship between mental ability and P3a is at variance to that observed for P3b. While the relationship between P3b and cognitive ability is consistent under identical experimental procedure, with a positive correlation with amplitude and a negative correlation with latency, the link between intelligence and P3a is much more unclear. DePascalis and colleagues (2008) have reported that the P3a response they measured did not differ between groups with a high and a low intelligence. Thus, the initial attention allocation seems to be comparable, despite the differences in the psychometric level. However, this statement is weakened by the fact that the amplitude of the P3a in this study shows a progressive increase from frontal to parietal locations. This relationship suggests that a maximal amplitude for this component was observed over parietal cortex and this response should be labeled rather P3b instead of P3a.

The purpose of the present study is to examine the relationship between basic characteristics of both P3 subcomponents, elicited in the active version of a three-tone oddball paradigm, and the psychometrically determined level of cognitive abilities. A three-stimulus oddball task is used to separate P3a from P3b (Comerchero and Polich, 1999; Katayama and Polich, 1999; Polich, 1998; Wronka, Kaiser and Coenen, 2008), which is not so easy with a two-stimulus task (Polich, 1998). All auditory stimuli are presented without backward masking according to the suggestion that the classical oddball paradigm is successful in differentiating subjects with different intelligence (Beauchamp and Stelmack, 2006). The instruction to the participants required a mental counting instead of motor response, in order to minimize a temporal overlap between P3a and P3b. It is expected that higher amplitude of P3b should be obtained for those subjects with higher cognitive abilities. A difference was expected for the target and the non-target stimuli. Moreover, it is expected that P3a should be more evident in the higher ability groups, what might reflect a more intense attention involvement in early stages of stimulus processing. It is finally anticipated that latencies of both P3 components will be shorter for the group scoring higher on Raven's APM.

## Methods

### Subjects

Twenty seven students (20 females & 7 males, mean age = 21.3 yrs, S.D.=1.45 yrs) participated in the experiment. All of them were right-handed and had normal, or corrected to normal, vision, as well as normal hearing. All reported to be free from neurological or psychiatric disorders, with an absence of drug abuse and medication. Students signed an informed consent and received course points for their participation. Subjects performed their tasks during two sessions (RAMP & EEG), scheduled at the same day, with an hour break in between the two 20- minutes sessions.

### Assessment of psychometric intelligence

The individual form of the Raven's Advanced Progressive Matrices (RAPM) was used. The RAPM scores were roughly normally distributed (skewness=−0.57; kurtosis=−0.32), with a range of 16–29. The RAPM scores (M=24.2, SD=3.3) were used to create two groups with a higher and a lower psychometric intelligence. The high ability (HA) group (n=13) scoring higher than the median (Md=24) and the low ability (LA) group (n=14) scoring lower than, or equal, to the median (M=27.1, SD=1.0, and M=21.6, SD=2.2, respectively for raw scores of the HA and LA group). Both groups had a quite similar mean age (M=21.0, SD=1.4, and M=21.5, SD=1.5, respectively).

### Stimuli

During EEG sessions participants were presented with random series of tones, consisting of standard 1 kHz, target 1,1 kHz and non-target 1,2 kHz tones, with probabilities of .80, .10 and .10 respectively. The task was to silently count the target tones and report the number at the end of the session. Stimuli were presented with random ISI (1.25 s – 2 s) through a loudspeaker located in front of the subject at 65 dB SPL, with 100 ms duration with 10-ms rise/fall time.

### Recording conditions

EEG was recorded using a BioSemi Active-One system from electrodes placed on the scalp using an Electro-Cap. Two additional electrodes, a common mode sense (CMS) active electrode and a driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively (cf. www.biosemi.com/faq/cms&drl.htm). The EOG was monitored by 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. EEG and EOG recordings were sampled at 512 Hz. The EEG was separated into epochs of 1000 ms duration, synchronized with the stimulus onset,

containing 100 ms pre-stimulus activity. Each epoch was baseline corrected using a 100 ms pre-stimulus baseline, filtered (band pass 0.01–35 Hz, 24 dB/oct), and re-referenced to average reference. Trials containing blinks and eye movements were corrected (Gratton, Coles and Donchin, 1983).

**Data analyses**

The P3 amplitudes were measured on difference waveforms, calculated by subtracting the average ERP elicited by the standard stimuli from that elicited by the target or non-target stimuli (Wronka, Kaiser and Coenen, 2008). Components were defined as the largest positive-going peaks within a specific latency window: 250-350 ms and 300-600 ms for the P3a and P3b respectively. These windows were selected on the basis of visual inspection of grand averaged ERP obtained for each condition. Peak amplitude was calculated relative to the pre-stimulus baseline. Repeated-measures analyses of variance (ANOVA) were performed examining the effect of within-subjects factor of STIMULUS type (target vs. non-target) on P3 amplitude, as well as the between-subjects factor of RAPM scores (HA vs. LA).

The sources of bioelectrical activity were estimated using the 2008 version of sLORETA (free academic software available at http://www.uzh.ch/keyinst/loreta.htm). The sLORETA images reflect the three-dimensional distribution of current density. The current implementation of sLORETA used the three-shell realistic head model (Fuchs et al., 2002) and electrode coordinates provided by Jurcak (Jurcak, Tzuzuki and Dan, 2007). All computations were made using the template from Montreal Neurological Institute MNI (Mazziotta et al., 2001), with the three-dimensional solution space restricted to cortical gray matter and hippocampus, as determined by the probabilistic Talairach atlas (Lancaster et al., 2000). The intracerebral volume is partitioned in 6239 voxels at 5 mm spatial resolution. The sLORETA images represent the standardized electric activity at each voxel in neuroanatomic MNI space as the exact magnitude of the estimated current density. Anatomical labels as Brodmann areas are also reported using MNI space, with correction to Talairach space (Brett, Johnsrude and Owen, 2002). The full description of the method can be found in (Pascual-Marqui, 2002). The proof of its exact, zero-error localization property is described in (Pascual-Marqui, 2007) and (Pascual-Marqui, 2009).

Current source density for the P3a component was defined as the mean value between 250 and 350 ms, and for the P3b component – between 300 and 600 ms. Statistical significance of intelligence-related differences in the current source density was assessed with statistical nonparametric mapping tests for independent samples, implemented in the version of LORETA used.

## Results

The P3a amplitude obtained in response to target stimuli was significantly smaller when compared to the P3a evoked by non-target stimuli [F(1,25)=11.97 p=.002]. In both cases, maximal amplitudes were recorded at vertex (Fig. 16). The P3a amplitude measured in the HA group was significantly larger in comparison to the P3a obtained from LA participants [F(1,25)=5.14 p=.032]. A similar pattern of differences is observed for target and non-target P3a, which is confirmed by a non-significant STIMULUS × RAPM interaction [F(1,25)=1.53 p=.228].

The amplitude of the target P3b was significantly larger when compared to the P3b evoked by non-target stimuli [F(1,25)=19.31 p<.001]. The P3b amplitude measured at midline parietal Pz electrode in the HA group was larger in comparison to the P3b obtained from LA participants [F(1,25)=5.64 p=.026]. A similar pattern of between subject differences was observed for target and non-target P3b, which was confirmed by a non-significant STIMULUS × RAPM interaction [F(1,25)=0.50 p=.486].

| Comparison | Brain area | BA | MNI coordinates | | | t-score |
|---|---|---|---|---|---|---|
| | | | X | Y | Z | |
| target P3a (200-350 ms) | right preCentral Gyrus | 6 | 30 | -15 | 65 | 3.49 |
| | right Middle Frontal Gyrus | 6 | 25 | -15 | 65 | 3.46 |
| | right Cingulate Gyrus | 31 | 10 | -30 | 45 | 3.39 |
| | right preCuneus | 7 | 5 | -35 | 45 | 3.38 |
| | right Superior Frontal Gyrus | 6 | 25 | -10 | 70 | 3.37 |
| | right Medial Frontal Gyrus | 6 | 10 | -25 | 50 | 3.36 |
| | right paraCentral Lobule | 6 | 5 | -30 | 50 | 3.35 |
| | left preCuneus | 7 | -5 | -35 | 45 | 3.32 |
| | left Cingulate Gyrus | 31 | -5 | -30 | 45 | 3.30 |
| | left paraCentral Lobule | 5 | -5 | -35 | 50 | 3.27 |
| target P3b (300-600 ms) | left Cingulate Gyrus | 23 | -5 | -30 | 30 | 3.66 |
| | left Posterior Cingulate Gyrus | 23 | -5 | -30 | 25 | 3.60 |
| | right Cingulate Gyrus | 23 | 5 | -25 | 30 | 3.59 |
| | right Posterior Cingulate Gyrus | 23 | 5 | -30 | 25 | 3.50 |
| | left preCuneus | 7 | -5 | -35 | 45 | 3.47 |
| | ParaCentral Lobule | 31 | 0 | -30 | 45 | 3.41 |
| | left ParaCentral Lobule | 31 | -5 | -25 | 45 | 3.38 |

Table 9. Results of sLORETA analysis of differences in brain activation between HA and LA groups obtained for target P3a and target P3b (p > .05). Brain regions were higher activity was obtained in HA subjects are presented along with stereotactic MNI coordinates.

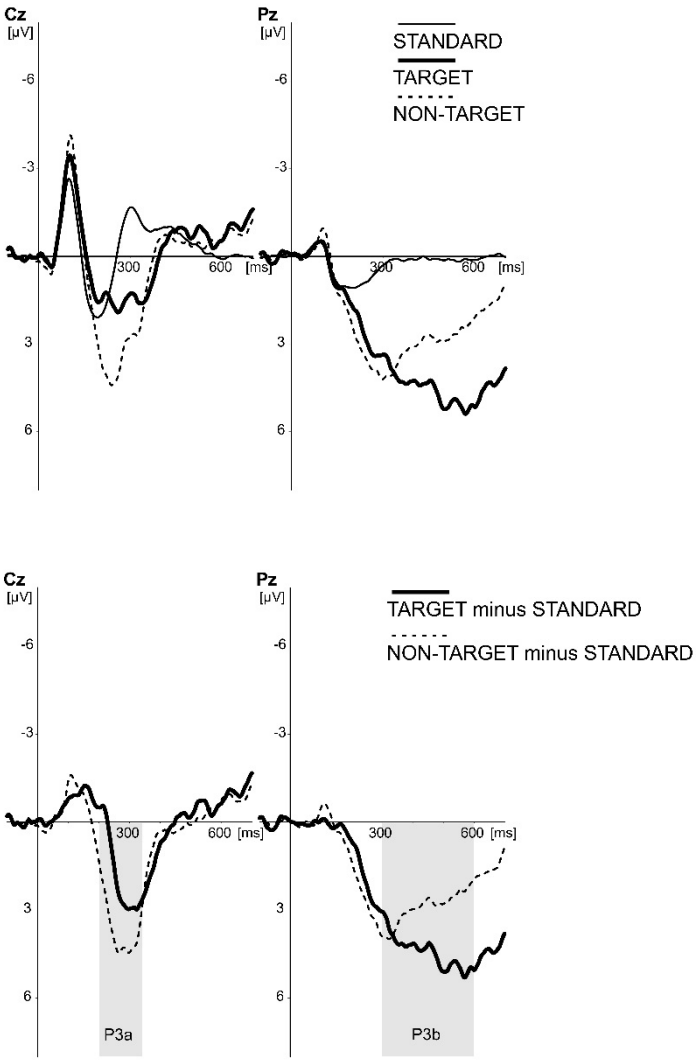


Figure 16. Grand average ERPs recorded in response to standard (thin black line), target (thick black line), and non-target tones (dashed line) from midline electrodes Cz and Pz (top panel). Grand average difference waves illustrating P3a and P3b responses from midline electrodes Cz and Pz. Thick black line represents target minus standard difference, and dashed line represents non-target minus standard difference (bottom panel).

Results from sLORETA indicate that targets and non-targets produced widespread activation in frontal, parietal, temporal and occipital brain areas between 250 and 350 ms after stimulus onset (P3a latency window). Direct between-group comparison revealed several brain areas where significantly higher activation was observed for subjects scoring high in RAPM. When responses to target were analyzed the effect was located in right frontal lobe. Stronger effect was obtained for brain responses to non-targets within the P3a latency window. Significant differences were located bilaterally in frontal lobe and in adjacent parietal cortex. Similarly, the effect of intelligence was observed for P3b latency window (300-600 ms) either. When responses to targets were analyzed stronger activation in frontal and parietal region was obtained for subjects scoring higher in RAPM. Analogous effect was not found when activity elicited by non-targets was analyzed. These effects are summarized in Table 9.

## Discussion

The experimental instruction provoked to allocate voluntary attention resources to the discrimination of auditory stimuli, but a response was only required for the infrequently presented targets. This manipulation allowed an effective differentiation of the P3 complex into two separate components: the earlier P3a and the later P3b. While the P3a peaked maximally over fronto-central locations, the P3b demonstrated parietal maxima. But what is even more important is that the magnitude of P3b to relevant target stimuli is generally larger than for non-target tones. This result is consistent with studies in which a three-stimulus oddball paradigm is used (Comerchero and Polich, 1999; Katayama and Polich, 1999; Wronka, Kaiser and Coenen, 2008). It is also consistent with Näätänen's suggestion that the generation of P3b is a match between the neuronal model of perceived stimulus and the voluntarily maintained attentional trace to a relevant event (Näätänen, 1990). Contrary to this, the P3a response to non-target stimuli was greater than the response to target stimuli. These results extend previous findings and suggest that the magnitude of the P3a is consistently related to the size of stimulus deviation from standard stimuli (Comerchero and Polich, 1999; Katayama and Polich, 1999; Wronka, Kaiser and Coenen, 2008). Hence, the results of the present experiment support the thesis that the early frontal P3a and the late parietal P3b reflect two different sets of physiological and psychological processes. The P3a amplitude could therefore illustrate the intensity of initial attention engagement (Wronka, Kaiser and Coenen, 2008). The larger the mismatch between the presented stimulus and the passively formed neuronal trace, the more intense is the involuntary attentional switch toward the new event and the more pronounced is the electrophysiological correlate, the P3a component

(Näätänen, 1990). The P3b amplitude could reflect an amount of attention resources voluntary allocated to the process of stimulus evaluation (Kok, 2001).

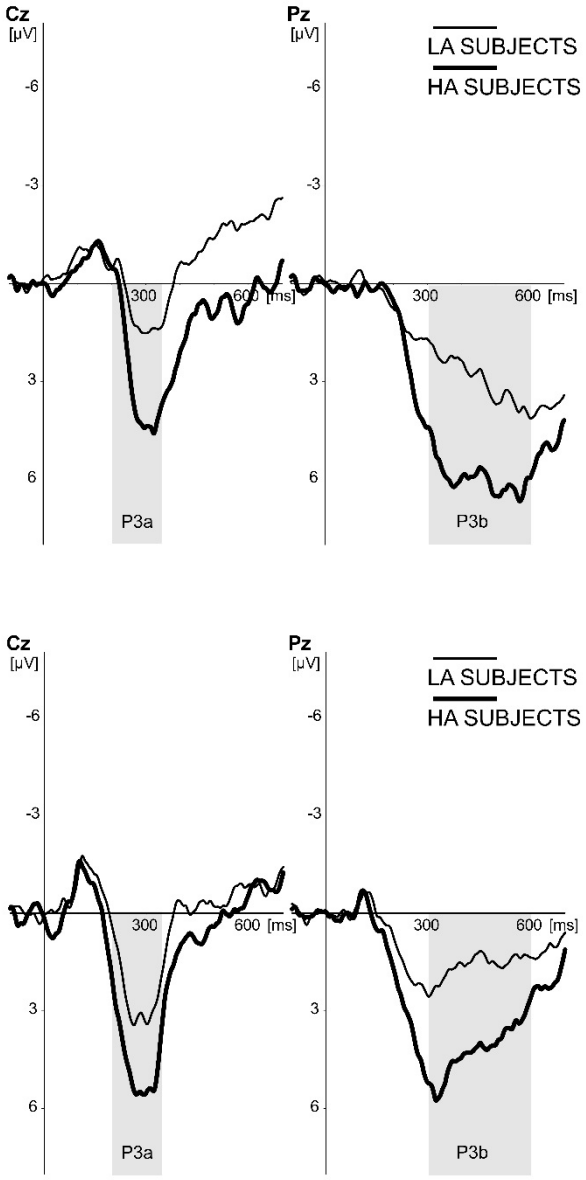


Figure 17. Grand average difference waves obtained as the responses to target (top right panel) and non-target (bottom right panel) for low ability (LA) and high ability (HA) groups.

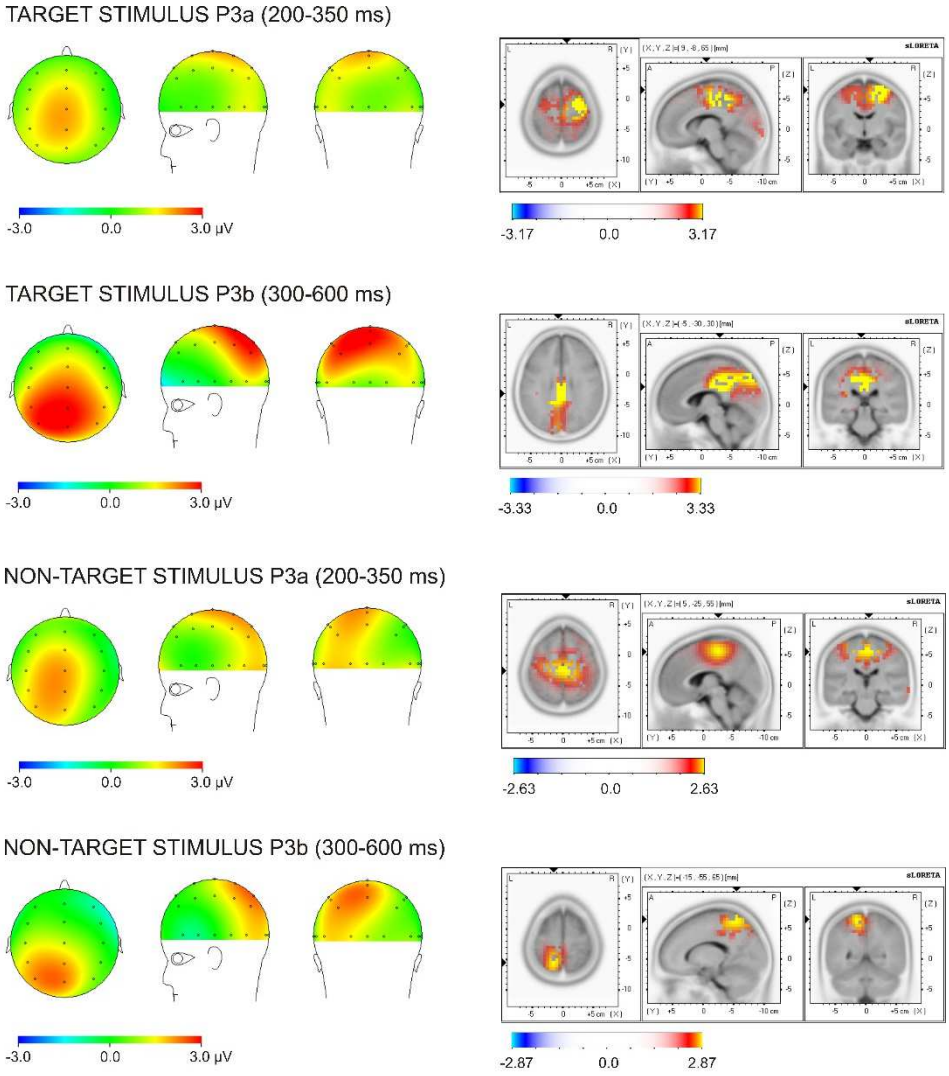


Figure 18. ERP splinemaps showing voltage differences in P3 amplitudes: HA group > LA group (left panel) and corresponding sLORETA three dimensional maps of voxel-by-voxel t-statistics representing differences in estimated brain activity (right panel) where depicted brain areas were more activated for HA group. Note that sLORETA analyses of non-target responses brought no significant results ($p<.05$ at t-threshold 3.21, 3.36, 3.12 and 3.33 for target P3a & P3b and non-target P3a & P3b, respectively).

The present results show that the amplitude of both components are sensitive to differences in cognitive abilities and that the amplitude is higher for the group scoring higher on Raven APM. This finding extends previous results (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008), and indicates that higher mental abilities, as defined by psychometric intelligence tests, are closely related to a greater ease in voluntary stimulus discrimination reflected in the P3b amplitude. Similar differences were obtained for target and non-target stimuli, what might suggest that the relationship between P3b amplitude and intelligence is independent of the objective stimulus meaning. This outcome supports also previous findings that the target and non-target stimuli in the auditory modality elicit a P3b component within a similar neural generator (Katayama and Polich, 1999; Wronka, Kaiser and Coenen, 2008; 2012).

Greater P3a amplitude in the group with higher scores on RAPM is also found. Importantly, a similar pattern of differences is observed for target tones as well as for non-target stimuli. It is reasonable to conclude that this effect could indicate that higher cognitive abilities are related to more intense initial attention engagements, provoked by significant mismatches between the presented stimulus and the passively formed neuronal traces of previous stimuli. This effect is at variance with previous findings (DePascalis, Varriale and Matteoli, 2008), where no intelligence-related differences in magnitude of the P3a response are reported. This inconsistency could be explained, at least partially, by main differences in the topography of P3a component in both studies. The P3a measured in the present study peaked maximally over fronto-central electrode location, what is consistent with many previous reports (Polich, 2007; Polich and Criado, 2006; Yamaguchi and Knight, 1991), while DePascalis and colleagues found a P3a maximum over parietal sites. Although the precise location of the neural generator of P3a is still unknown, the frontal cortex and anterior part of the cingulate gyrus seem to be the best candidates, because P3a is markedly affected by frontal lesions. Also a positron emission tomography (PET) study using a three-tone task reports that P3a amplitude is positively correlated with activity within the anterior cingulate cortex (Ebmeier et al., 1995).

The analysis of the event-related potentials measured here demonstrates that processes related to both the initial stage of attention engagement, as indexed by P3a, and the later stimulus evaluation and classification, reflected in P3b, are more intense in subjects scoring higher in an intelligence test. The effects of mental abilities observed in this study could be related to differences in frontal and parietal brain regions. This is consistent with results from neuroimaging study of Grey, Chabris and Braver (2003) who found that relationship between Raven's score and accuracy in an n-back task could be explained by activities in frontal and parietal lobes, and is also in line with Haier and

colleagues (2004) report that cognitive abilities can be related to variation in brain structures within frontal and parietal lobes. Our findings are also in line with data reported from studies on abstinent alcoholics (Hada et al., 2000; 2001) and frontal patients (Yamaguchi and Knight, 1991). Cognitive problems in long-term alcoholics as well as in frontal patients could be observed in sensory discrimination and attention functioning. At the same time, amplitudes of both P3a and P3b are diminished in these groups in comparison to the matched controls. All these studies, but in particular the results of the present study suggest that activities in frontal and parietal brain areas are closely related to cognitive abilities, and the nature of this relationship is a relevant topic for future research.

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# CHAPTER 6

## Intelligence and ERP responses measured in Ericksen Flanker Task *

**Abstract**

The aim of the study was to establish the relationship between fluid intelligence, measured with the Raven's Advanced Progressive Matrices (RAPM), and patterns of brain activity in task engaging attention. Subjects were presented with the Ericksen Flanker Task while the Event-Related Potentials (ERP) were measured. We found that higher fluid intelligence can be linked with more efficient detection of conflict. This was reflected in a more differentiated N2 amplitude, in comparison to lower intelligence group. Additionally, larger amplitude of the P3 component was measured from subjects scoring higher on RAPM. The effects on N2 and P3 indicate a presumable link between the activities of the frontal and parietal lobes, and suggest that these activities are closely related to cognitive abilities, expressed in the psychometrical determined intelligence. In short the present results suggest that a high level of cognitive ability is closely related to an efficient functioning of the attention mechanism.

### Introduction

Recent neuroimaging and electrophysiological studies show that there is a consistent relationship between the level of fluid intelligence and functioning of some specific brain regions. Findings from these studies indicate that a higher intelligence can be associated with enhanced activation within the frontal and parietal cortical regions. Specifically, Gray, Chabris & Braver (2003) found that the level of cognitive abilities can be closely related to the activity within the frontal and the parietal lobes during demanding tasks engaged in working memory. They reported that the relationship between score on Raven's Progressive Matrices and accuracy in an n-back task depend almost entirely on activation of these brain areas.

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The role of the frontal and parietal cortical areas was also accentuated by Prabhakaran et al. (1997), who compared fMRI responses measured when subjects were performing two differently g-loaded tasks. The results obtained by these authors indicate that the prefrontal cortex, together with the superior parietal region, is highly relevant for fluid reasoning. A similar conclusion was drawn by Duncan et al. (2000), who measured PET responses in two differently g-loaded tasks. The authors reported that a higher brain activity in the task was highly correlated with standard measures of fluid intelligence when compared to a task with lower g-load. Significant effects were observed for brain areas located in the lateral and the medial frontal cortex, the parietal lobe, and the occipital cortex. The effect was additionally confirmed by Lee et al. (2006), who found a greater bilateral activity in the lateral prefrontal, the medial frontal and the parietal areas when a complex high g-loaded task was compared with a much simpler one. Findings from these experiments suggest the relevance of the frontal and the parietal cortical regions in tests reflecting fluid intelligence.

Results from human electrophysiological studies lead to similar conclusions. Consistently, a greater amplitude of the P3 component of the ERP was found in high IQ subjects in comparison to low IQ participants (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; Fjell et al. 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002; Wronka, Kaiser and Coenen, 2013). It is worth to be noted that the P3 component represents activity of numerous widely distributed brain areas (Polich and Criado, 2006; Polich, 2007). Previous reports suggest that the frontal and the parietal cortical regions contribute mainly to the scalp recorded P3 component. Findings from patients with frontal or temporo-parietal lesions indicate a link between the process of P3 generation and activity of these brain regions (Yamaguchi and Knight, 1991a; 1991b). This hypothesis is also supported by Halgren and colleagues (1995) with findings from intracerebral recordings in patients. This is also consistent with recent functional imaging studies (Bocquillon et al., 2011). Similar results were also obtained using source localization methods. Recently, Wronka, Kaiser and Coenen (2012) have localized neural generators of the P3 component using the standardized low resolution electromagnetic tomography (sLORETA). They reported that the lateral frontal cortex, the cingulate gyrus and the parietal lobe are the major sources of P3. What should be noticed is that they found in a subsequent study that differential activity measured within these brain structures could be linked with intelligence-related differences in the scalp recorded P3 amplitude (Wronka, Kaiser and Coenen, 2013).

Taken together, all these studies provide evidence that the level of fluid intelligence can be closely related to the activation of fronto-parietal network (Jung and Haier, 2007). Neuroimaging studies indicate that this network consist of at least three distinct brain regions, namely the lateral prefrontal cortex, the cingulate gyrus and the

parietal lobe (Gray, Chabris and Braver, 2003; Duncan et al., 2000; Lee et al., 2006; Prabhakaran et al., 1997). There is a general agreement that the prefrontal cortex, along with the cingulate gyrus and the parietal cortex, forms the network involved in various higher cognitive functions including attention, working memory, language production and memory retrieval. Therefore, it is reasonable to assume that the fronto-parietal network forms the neural basis of processes closely linked to general intelligence factor. This is consistent with the notion that the same group of brain structures can be involved in the generation of the P3 component (Wronka, Kaiser and Coenen, 2012), which is known to be sensitive to individual differences in cognitive abilities (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Wronka, Kaiser and Coenen, 2013).

However, this conclusion is weakened by the fact that rather simple experimental paradigms, such as variations of the auditory oddball task, have been utilized to measure P3 in most of the ERP studies (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Wronka, Kaiser and Coenen, 2013). In contrast to this, much more complex tasks, engaging working memory or cognitive control, have been used in neuroimaging studies (Gray, Chabris and Braver, 2003; Duncan et al., 2000; Lee et al., 2006; Prabhakaran et al., 1997). Therefore it is not completely clear whether results obtained with neuroimaging techniques and the scalp-recorded P3 component actually correspond to the same phenomenon. Moreover, the majority of the neuroimaging studies uses visual material, while the ERP research utilize mostly the auditory modality.

The purpose of the present study was to determine the relationship between the psychometrically determined level of cognitive abilities and the electrophysiological indexes of fronto-parietal activity measured in a visual task. Instead of the rather simple oddball paradigm, we used Ericksen Flanker Task. In this task, participants respond with a left or right button press to the central letter of a five-letter display; flanking letters can be the same as the central letter or associated with the opposite response (e.g., if a central H signals a right-hand response and S a left-hand response, then HHHHH is a congruent array and SSHSS an incongruent array for a right-hand response). This paradigm demands cognitive operations like detection of the response conflict, which is closely related to stimulus congruency, and the subsequent resolving of the conflict. The compatibility effect can be reflected in slower responses to the incongruent arrays. Electrophysiological findings suggest that the interference effect in the Flanker Task can be linked with the difference in amplitude of the N2 component. Specifically, a larger negative deflection at frontocentral locations, beginning 200 ms after stimulus, can be observed in response to incongruent trials in comparison to congruent trials (Bartholow et al., 2005; Folstein and Van Petten, 2008; Heil et al., 2000; Kopp, Rist, & Mattler, 1996).

Findings from studies using dipole source modelling have suggested that flanker N200 can be linked with differential activation in the anterior part of the cingulate gyrus (Liotti et al., 2000; van Veen & Carter, 2002a, 2002b). Additionally, the interference effect can be also associated with the difference in latency or amplitude P3 component. Relative to congruent trials, incongruent trials elicit a delayed parietal P3 (Folstein and Van Petten, 2008) with lower amplitude (Davies et al., 2001).

We expected that higher cognitive abilities, measured with the Raven Progressive Matrices, are associated with more effective cognitive control (Engle and Kane, 2004). This can be reflected in more efficient detection of response conflict, and in more effective resolving of this conflict, which can be associated with precise stimulus evaluation. Therefore, it can be assumed that individual differences in fluid intelligence can influence the brain activity corresponding to these processes. Conflict detection can be linked with the N2 effect, where enhanced negativity is observed in incongruent trials in comparison to congruent ones. Recent findings suggest that N2 effect in the Flanker Task is generated in the cingulate cortex (van Veen & Carter, 2002a, 2002b). Intelligence related differences in activation of the cingulate cortex were previously reported using neuroimaging techniques (Duncan et al., 2000; Gray, Chabris and Braver, 2003; Lee et al. 2006; Prabhakaran et al., 1997) and electrophysiological methods of ERP source localization (Wronka, Kaiser and Coenen, 2013). Due to this, it is reasonable to expect that this part of the brain can be dissimilarly engaged in high and low ability subjects in the face of response conflict in Flanker Task. This difference can be reflected in various N2 effects obtained for low and high IQ. We expected a greater N2 effect in subjects scoring higher on Raven's test. Moreover, it was anticipated that the P3 component should be more evident in higher ability groups, which might reflect a greater ease in voluntary stimulus discrimination. Similar effects were previously reported in many studies using oddball paradigms (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; Fjell et al. 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002; Wronka, Kaiser and Coenen, 2013).

## Methods

### Subjects

Twenty two students (18 females & 4 males, mean age = 21.4 yrs, S.D.=1.47 yrs) were recruited from introductory psychology classes. All participants were right-handed and had normal, or corrected to normal, vision, as well as normal hearing. All of them reported to be non-smokers with no reported history of drug abuse or neurological disorders.

Students signed an informed consent and received course points for their participation. Subjects performed their tasks during two 30-minutes sessions (RAMP & EEG), scheduled at the same day, with an hour break in between.

**Assessment of psychometric intelligence**

The individual form of the Raven's Advanced Progressive Matrices (RAPM, Raven, Court & Raven, 1983) was used. The RAPM scores were roughly normally distributed (skewness=−0.24; kurtosis=−1.24), with a range of 20–29. The RAPM scores (M=24.6, SD=2.7) were used to create two groups with a higher and a lower psychometric intelligence. The high ability (HA) group (n=11) scoring higher than the median (Md=25) and the low ability (LA) group (n=11) scoring lower than, or equal, to the median (M=22.3, SD=1.5, and M=27.0, SD=1.0, respectively for raw scores of the LA and HA group). Both groups had a quite similar mean age (M=21.5, SD=1.5, and M=21.2, SD=1.5, respectively).

**Procedure**

During EEG sessions participants were asked to restrict body movements and blinking as much as possible. On each trial a five-letter string was presented (Ericksen Flanker Task, Ericksen and Ericksen, 1974). The stimuli used for targets and flankers were the letters H and S. The central letter was the target, the remaining letters the flankers. On congruent trials, the target letter was identical to the flankers (SSSSS of HHHHH); on incongruent trials, the target letter differed from the flankers (SSHSS or HHSHH). This resulted in 4 possible target-flanker combinations.

Subjects were instructed to respond to target stimuli using a computer keyboard. If the centrally presented letter was H, they should press a key on the left side of the keyboard with their left index finger. Alternatively, if the target was the letter S, they should press a key on the right side of the keyboard with their right index finger. In order to control for lateral bias in the motor response, left- and right-hand responses were counterbalanced across subjects.

The stimuli were presented on a 17” PC monitor. The letters were white against a black background. Each trial began with a 500-ms presentation of the fixation cross. Flankers were presented 100 ms prior to the onset of target letter. Target and flankers disappeared simultaneously when the response was made, but no later than 1000 ms after target onset. The interval between subject’s response and the beginning of the next trial was 1500 ms. Trials were presented in random order with identical probability.

**Recording conditions**

The EEG was recorded using a BioSemi Active-One system from 32 electrodes placed on the scalp using an Electro-Cap. Two additional electrodes, a common mode sense (CMS)

active electrode and a driven right leg (DRL) passive electrode, were used as reference and ground electrodes, respectively (cf. www.biosemi.com/faq/cms&drl.htm). The EOG was monitored by 4 electrodes, placed above and below the right eye and in the external canthi of both eyes. EEG and EOG recordings were sampled at 512 Hz. The EEG was separated into epochs of 700 ms duration, synchronized with the stimulus onset, containing 150 ms pre-stimulus activity. Each epoch was baseline corrected using a 150 ms pre-stimulus baseline, filtered (band pass 0.01–30 Hz, 24 dB/oct), and re-referenced to average reference. Trials containing blinks and eye movements were corrected (Gratton, Coles, & Donchin, 1983).

**Data analyses**

For the different target-flanker combinations, mean reaction times (RTs) were calculated. Correct reactions occurring within a 150–1200 ms interval after stimulus presentation were considered as hits. The percentage of errors and misses were also determined. Because misses were very rare, we will focus here on hits and errors. Behavioral results, RTs and error rates were analyzed using repeated-measures analysis of variance (ANOVA), examining the effects of within-subject factor of STIMULUS congruency (congruent *vs*. incongruent) and between-subjects factor of RAPM scores (HA *vs.* LA).

The ERP components were defined as the mean voltage within a specific latency windows: 270-320 ms and 330-400 ms for the N2 and P3, respectively. These windows were selected on the basis of visual inspection of grand averaged ERP obtained for each condition. Amplitudes of the N2 and P3 components were calculated relative to the pre-stimulus baseline. Peak latencies of the N2 and P3 components were measured from the stimulus onset within the same latency windows as provided above. Repeated-measures analyses of variance (ANOVA) were performed examining the effect of within-subject factor of STIMULUS congruency (congruent *vs*. incongruent) on N2 & P3 amplitude and latency as well as the between-subjects factor of RAPM scores (HA *vs.* LA). Analysis of N2 component was restricted to vertex (electrode Cz). Analysis of the P3 component was performed for the parietal electrode Pz.

## Results

**Analysis of behavioral data**

Subjects were slower on incongruent (M=516.2 ms; SD=71.9) than on congruent (M=502.4 ms SD=61.6) trials in the Flanker Task. However, the difference did not reach the level of significance [$F(1,20)=3.01$, $p=.098$]. Similar pattern of differences were obtained for both groups differentiated by their RAPM scores (congruent trials: M=505.4

ms SD=61.9 and M=499.4 ms SD=64.2; incongruent trials: M=519.3 ms SD=70.1 and M=513.1 ms SD=77.0 for HA and LA subjects, respectively). This was confirmed by non-significant STIMULUS by RAPM interaction [F(1,20)<0.01, p=.987]. Subjects in both groups respond equally fast [F(1,20)=0.05, p=.832].

The mean error rate was very small (<1%) and was comparable for congruent (M=0.3; SD=1.0) and incongruent trials (M=0.2; SD=0.5). This leads to non-significant main effect of STIMULUS congruency [F(1,20)=0.93 p>.3]. Correspondingly, analysis of STIMULUS by RAPM interaction [F(1,20)=3.12 p=.093] as well as main effect of intelligence [F(1,20)=1.60 p>.2] brought no significant results.

**Analysis of electrophysiological data**

Grand average ERPs obtained at electrodes Cz and Pz in two conditions (congruent and incongruent) plotted separately for groups scoring high and low in RAPM are presented in figure 19.

*N2 component*

Amplitudes of N2 component measured in response to congruent and incongruent trials were comparable, which resulted in a non-significant main effect of STIMULUS congruency factor [F(1,20)=0.32 p>.5]. However, congruency effects were found to be different for HA and LA subjects, which was reflected by significant interaction between STIMULUS congruency and RAPM [F(1,20)=9.06 p=.007]. Enhanced negativity within the latency window of the N2 component was recorded for incongruent trials for the group scoring higher on RAPM (M=3.2 μV; SD=3.9 and 1.8 μV; SD=3.1 for congruent and incongruent trials, respectively). Difference in opposite direction was found for LA subjects (M=–0.8 μV; SD=4.2 and 0.2 μV; SD=4.1 for congruent and incongruent trials, respectively). This effect is presented in figure 20. At the same time, we found that overall N2 amplitude recorded for the LA group tended to be lower in comparison to the HA group. However, this difference did not reach the level of significance [F(1,20)=3.06 p=.095].

A similar analysis was performed for latencies of the N2 component. We found that the N2 component measured in response to congruent trials tended to peak earlier in comparison to incongruent trials [F(1,20)=3.80 p=.065]. This effect was comparable for HA and LA subjects, as it is revealed by non-significant STIMULUS by RAPM interaction [F(1,20)=0.37 p>.5]. Simultaneously, latencies of N2 obtained for HA and LA subjects were comparable, which resulted in a non-significant main effect of RAPM [F(1,20)=0.92 p>.3].

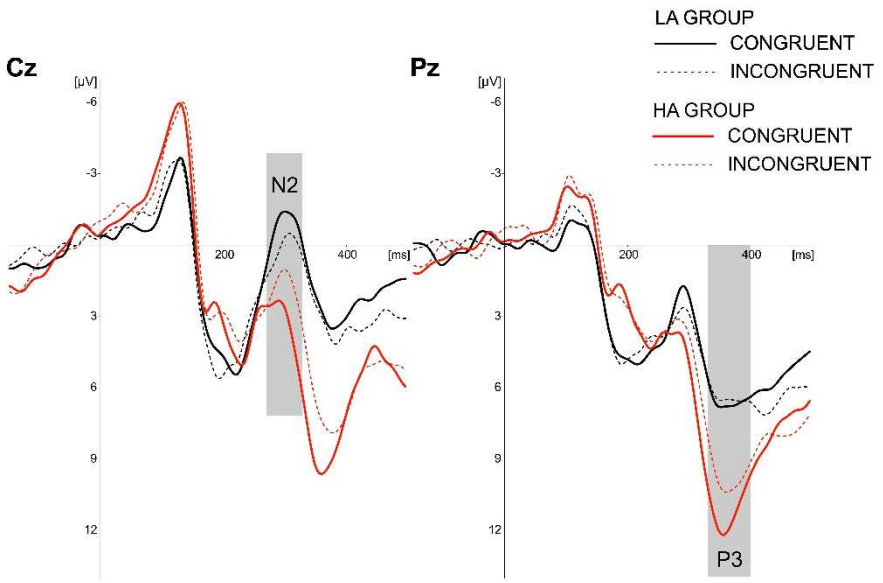


Figure 19. Grand average ERPs recorded in response to congruent (solid line) and incongruent stimuli (dashed line) from midline electrodes Cz and Pz plotted separately for low ability group (black lines) and high ability group (red lines).

*P3 component*

A significant main effect of STIMULUS congruency was found when amplitudes of P3 component were analyzed [F(1,20)=6.23 p=.021]. Higher values were obtained in response to congruent in comparison to incongruent trials. The same pattern of results was observed for both groups differentiated by RAPM scores. However, the congruency effect, reflected in differences in P3 amplitude, was observed to be stronger for HA subjects. This conclusion was supported by almost significant STIMULUS by RAPM interaction [F(1,20)=3.90 p=.062]. Moreover, we also found that amplitude of P3 component differed significantly between these two groups. Higher values were recorded for HA subjects, which was reflected in significant main effect of RAPM [F(1,20)=4.33 p=.050]. This difference is illustrated in figure 20.

A similar analysis performed on P3 latencies brought no significant results. We obtained no effect of STIMULUS congruency [F(1,20)=1.51 p>.2], RAPM [F(1,20)=0.32 p>.5], as well as STIMULUS x RAPM interaction [F(1,20)=1.14 p>.2].

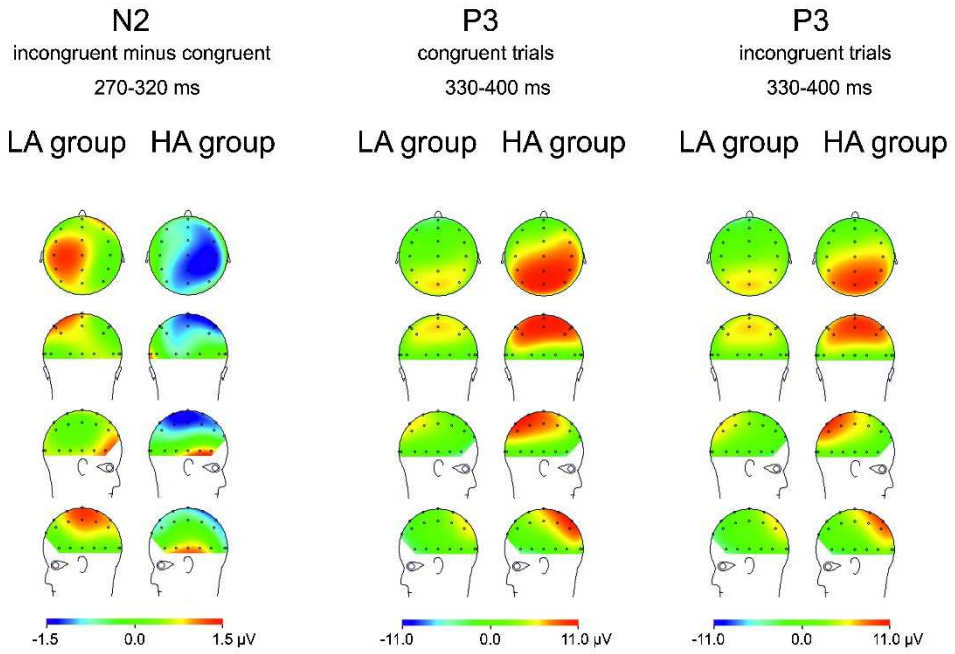


Figure 20. ERP splinemaps illustrating congruency effect (voltage differences: incongruent minus congruent trials) within the N2 latency window (left panel) and showing topography of the P3 reponse to congruent (middle panel) and incongruent trials (right panel). All splinemaps were plotted separately for group scoring high (HA) and low (LA) on RAPM.

## Discussion

The main aim of the present study was to establish the relationship between the psychometrically determined level of fluid intelligence and the electrophysiological indexes of the fronto-parietal network activity during task demanding response conflict detection and resolving. We found that subjects scoring higher on test of intelligence, differ significantly in the magnitude of the N2 effect from those obtaining lower intelligence scores. Specifically, the enhanced negativity within the latency window of the N2 component was obtained in response to incongruent trials when compared to congruent stimuli for subjects scoring higher on RAPM. This finding is consistent with results from many previous studies exploring electrophysiological correlates of conflict detection (Davies et al., 2001; Kopp, Rist and Mattler, 1996; van Veen and Carter, 2002a;

Folstein and van Petten, 2008). Such effect was virtually absent for low ability participants.

Several findings demonstrate that the N2 effect observed in the flanker task is elicited by the need to control incorrect response preparation (Bartholow et al., 2005; Gehring et al., 1992). Additionally, the probability of the response categories and of the congruent and incongruent trials is usually 50%, which eliminates the possibility that the frontal N2 is driven by different stimulus probability, as it is observed in the oddball task. Moreover, a computational model of conflict monitoring predicted that the N2 must be larger when measured in response to incongruent trials in comparison to congruent ones (Yueng et al., 2004). Finally, the dipole source for both the N2 to correct and incorrect responses were localized to cingulate cortex (van Veen and Carter, 2002a). Neuroimaging studies indicate that the anterior cingulate gyrus plays an important role in mediating response conflict in the flanker task (see Ridderinkhof et al., 2004, for a review). Some authors suggest that the lateral frontal cortex may also be involved in the selection of the correct response and the inhibition of incorrect ones (Aron et al., 2003; Aron, Robbins and Poldrack, 2004).

Results obtained in our study can therefore indicate that the level of fluid intelligence can determine the ability to detect response conflict and to inhibit initially incorrect motor response induced by incongruent trials. However, this conclusion is weakened by the fact that no between group differences were obtained at the behavioral level in our study. High ability participants did not differ from low ability subjects, neither in their reaction times or response accuracy. It is however probable that the task was relatively easy for both groups. This conclusion is based on the fact that error rates recorded in both groups were very low. Therefore it cannot be excluded that processes of conflict detection and selection of correct responses, reflected in the N2 effect, can differ between these groups, even when differences at the behavioral level are virtually absent.

Present results show also that the P3 component is sensitive to the differences in cognitive abilities, and that the amplitude is higher for the group scoring higher on RAPM. This finding is consistent with previous results (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; Fjell et al. 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002; Wronka, Kaiser and Coenen, 2013). All these studies have demonstrated that a higher level of fluid intelligence is closely associated with more effective stimulus discrimination reflected in P3. Moreover, in our present study we found also that similar between group differences can be obtained for congruent and incongruent trials, which may suggest that the relationship between fluid intelligence and P3 amplitude is independent of the stimulus response compatibility. This finding is consistent with results obtained by

Wronka, Kaiser and Coenen (2013), who reported a comparable intelligence effect for P3 amplitude measured in response to targets and non-targets in an auditory oddball task. It has to be noticed that results from electrophysiological and neuroimaging studies suggest that major neural generator has been localized in the parietal cortex (Bocquillon et al., 2011; Volpe et al., 2007; Wronka, Kaiser and Coenen, 2012; Yamaguchi and Knight, 1991b). Therefore it can be concluded that the activity of parietal area is more pronounced in subjects scoring higher on the IQ test. It is also worth to notice that in most previuos studies reporting positive relationship between measures of fluid intelligence and P3 amplitude, auditory oddball paradigm has been utilized. Results from present experiment indicate that similar effect can be observed in the case of visual stimuli.

## Conclusions

Results obtained in this study demonstrate that the processes associated with both the response conflict detection and stimulus evaluation or classification are enhanced in participants scoring higher on the IQ test. Response conflict detection can be reflected in the N2 effect, where amplitude of N2 component is greater when measured in response to incongruent trials thatn to congruent ones. This effect was found to be evident for participants scoring higher on RAPM and virtually absent in low ability subjects. This effect indicate that effectiveness of neural processes related to conflict detection is positively correlated with the level of fluid intelligence. Simultaneously, it was also found that P3 amplitude measured in response to letter strings in Flanker Task is greater for high IQ subjects. This finding might reflect a greater ease in voluntary stimulus discrimination in comparison to low IQ group. Effects of fluid reasoning observed in this study can be related to activity differences in the frontal and parietal brain regions. These findings confirm and extend results from Gray et al., 2003; Lee et al., 2006 and Haier and colleagues (Larson et al., 1995; Haier et al., 2004), all indicating a presumable link between the activity of frontal and parietal lobes and intelligence. The results of the present experiment, clearly suggest that the activities in frontal and parietal brain areas are closely related to cognitive abilities, expressed in the psychometrical determined intelligence.

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# CHAPTER 7

## GENERAL DISCUSSION

*"Intelligence is a very general capability that, among other things,*
*involves the ability to reason, plan, solve problems, think abstractly,*
*comprehend complex ideas, learn quickly and learn from experience.*
*It is not merely book learning, a narrow academic skill, or test-taking smarts.*
*Rather, it reflects a broader and deeper capability for comprehending*
*our surroundings—'catching on', 'making sense' of things,*
*or 'figuring out' what to do."*
(Gottfredson, 1997)

The fragment cited above stems from Linda Gottfredson's paper reporting opinions about the human intelligence gathered from a large number of intelligence researchers. This is an example that there is consensus that intelligence is a real psychological phenomenon. However, on the other hand the same fragment shows clearly how imprecise definitions of intelligence are.

Intelligence researchers accept the thesis that the brain functioning plays a central role in general intelligence, which is usually designated as 'g'. This point of view has its root in Spearman's model of intelligence (1904). He found that measures of performance in various cognitive tests show a pattern of almost universal positive correlation. People who perform well in one task or are good in one domain, also tend to perform well in many others. The same was observed in many later studies using several measures of cognitive abilities (Johnson, Nijenhuis and Bouchard, 2008). To explain this effect, Spearman put forward the hypothesis of a general factor (or 'g' factor), which contribute in diverse forms of cognitive activities being the source of the positive manifold effect. He additionally suggested that all mental performance can be conceptualized in terms of a single general ability factor ('g'), accompanied by larger number of specific factors. Spearman hypothesized that 'g' factor can be linked to brain physiology which he described as undefined 'mental energy'.

The concept of 'g' was later expanded by other researchers. Cattell and Horn have proposed that general intelligence can be linked to two factors indicated as 'fluid intelligence' and 'crystallized intelligence' (Horn and Cattell, 1966). The assumption that there is a link between brain functioning and the level of mental abilities seems to be

specifically true for the fluid intelligence, which refers to inductive, deductive, and quantitative reasoning with materials and processes that are new to the person doing the reasoning (Cattell, 1963). In contrast to this, the crystallized intelligence refers to the application of acquired knowledge and learned skills to answering questions and solving problems in the context of highly familiar materials and processes. Crystallized intelligence can easily be measured using tests of knowledge, general information, use of vocabulary, and a wide variety of acquired skills (Horn and Cattell, 1966).

There is agreement that crystallized intelligence can also be linked to some specific brain functions which are closely related to e.g. memory or the use of language. It should be however noticed that crystallized intelligence strongly depends on individual educational history and is influenced by several socio-economic factors. In contrast to this, fluid intelligence seems to be associated with abstract, nonverbal reasoning. Due to this, fluid intelligence cannot be related to specific skills learned acquired through acculturation, and therefore the relationship between fluid reasoning and brain activity should be far more nonspecific and domain-independent.

As it is presented in chapter 1 there is a group of theories trying to associate intelligence with specific features of brain functioning. Most of them are based on the supposition that basic properties of cognitive abilities which are closely linked to intelligence can be observed at the brain level. Due to this, differences in brain processes connected with those abilities can shed light on the biological basis of intelligence. According to this, several hypotheses have been proposed as a possible variable enabling explanation for individual differences in mental abilities.

Speed of neural transmission can be an example of such single variable which was supposed to be a basis of individual differences in intelligence at the biological level. However, as it is presented in introductory chapter, results from studies exploring the problem of the relationship between fluid intelligence and the speed of information processing are inconclusive. Specifically, no reliable relation between mental ability and the latency of early ERP components were found. At the same time however, findings from many studies (Ladish and Polich, 1989; O'Donnell et al., 1992; Polich et al., 1986; Polich, Howard and Starr, 1985; Polich and Martin, 1992; Walhovd and Fjell, 2002; Zurron and Diaz, 1998) show that high level of IQ can be associated with shorter latency of the P3, a component consistently related to attention, to decision making and to memory updating (Kok, 2001; Polich and Criado, 2006; Polich, 2007).

Another concept applied in explanation of biological basis of intelligence was the efficiency of transmission of nervous impulses (A.E. Hendrickson, 1982). At the empirical level this phenomenon is reflected in complexity of ERP responses measured as the ‘string length’ index (or ‘string measure’). Initial reports suggested that this measure can be a manifestation of the error-rate encountered during information transmission between

neurons (D. E. Hendrickson, 1982). It has also been observed that scores in intelligence tests correlate significantly with this index. However, the results of subsequent work varied considerably. Due to this, the 'string measure' was criticized for being highly non-specific and consequently not useful in pursuing an explanation of the relationship between structure and function of the human brain and intelligence (Burns, Nettelbeck and Cooper, 1997). The critique of the Hendrickson model was also provided by Robinson (Robinson, 1993; Robinson and Behbehani, 1997) who insisted that the measure was sensitive to so many factors and is therefore of little use, either practically or theoretically.

There is also a suggestion that differences in fluid intelligence are related to the brain efficiency, which can be reflected in various levels energy consumption or engagement of different number of neurons (Haier et al., 1988; 1992). According to this hypothesis, high fluid intelligence can be linked with the more economically functioning brain. Early studies provided evidence that persons scoring higher on IQ tests have demonstrated lower glucose metabolism within the brain when measured during performance of cognitive tasks. However, many later conducted neuroimaging studies delivered results which are at odds with this hypothesis.

Taken together, there is no generally accepted theory which can explain how the brain functioning can be related to fluid intelligence. Thus, a major neuroscientific challenge is to identify specific properties of the brain that are responsible for individual differences in intelligence. The current thesis is an attempt to investigate the relationship between fluid intelligence and the functioning of the neuronal correlates of the attention system. In order to achieve this, basic characteristics of the P3 component were used as indices of the early phase of attentional resource allocation and were compared between subjects distinguished by their score on psychometric tests of intelligence.

## P3 component as an index of attention

The aim of the first two experiments presented in the thesis was to investigate basic characteristic of P3 subcomponents. In the first experiment, P3 elicited by simple tones, presented alone or accompanied by the simultaneous exposition of neutral visual stimuli, was compared in active and passive conditions. The main question was whether visual stimulation will influence the auditory P3 recorded in active condition in the same way as in the passive one. The obtained results suggest that frontal and parietal P3 subcomponents reflect two distinct psychological and physiological processes. Specifically, the P3 recorded over the parietal cortex was strongly dependent on the voluntary attention engagement. An apparent P3 deflection was obtained at parietal locations only when attention was intentionally allocated to relevant auditory stimuli.

Importantly, parallel visual processing decreased the strength of this effect. Exposition of neutral picture which preceded presentation of auditory stimuli results in reduction of P3 response. It was concluded that available attention resources were assigned to the analysis of visual stimulus, and, thus, were not available to analyze the subsequent auditory stimuli. Similar phenomenon was also reported by several other authors (Cuthbert et al., 1998; Oray, Lu and Dawson 2002; Schupp et al., 1997).

In contrast to this, the frontal P3 component was enhanced when measured as a response to tones presented along with neutral pictures in comparison to exposition of auditory stimuli alone. A similar effect was observed in passive and active conditions. Moreover, when voluntary attention resources were provoked by the experimental instruction, a larger P3 response was produced at the frontal site, and this was evident both when tones were or were not accompanied by visual stimuli.

The exposition of neutral pictures has engaged the frontal lobe. Therefore, subsequently presented auditory stimuli evoked a stronger initial attention allocation reflected in an enhanced frontal P3, in comparison to auditory stimuli presented alone. Additionally, the frontal P3 was also significantly enhanced as the consequence of, presumably, a greater attentional focus in the active condition, which is supposed to evoke controlled processing. Obtained results provided evidence that both types of frontal responses, the involuntary shift in reaction to neutral pictures and the voluntary focus provoked by the instruction, are capable to increase the frontal P3 amplitude. Moreover, the outcome of the experiment supports the thesis that these two effects could be additive.

Results from the second experiment additionally supported the thesis that frontal and parietal P3 subcomponents are a sign of distinct psychological and physiological processes. Here, a three-stimulus oddball paradigm was employed in which subjects were presented with random sequence of tones while they performed a discrimination task in visual modality with no response to the tone (passive condition) or responded to an infrequently occurring target stimulus inserted into sequence of frequent standard and rare non-target stimuli (active condition). The results clearly showed that two different P3 subcomponents can be reliably related to activity of frontal and parietal region of the cerebral cortex. Specifically, it was found that the magnitude of the frontal P3 is determined by the relative perceptual distinctiveness among stimuli. Its amplitude was larger for those stimuli which differed more from the standard, while a similar effect was observed in passive and active task. Additionally, amplitude of this component was influenced by the strength of attentional focus, which was reflected by significantly larger response recorded in the active session than in its passive counterpart. The apparent parietal P3 responses were obtained only in the active condition. Here, we found larger P3 amplitude when obtained as a response to the target than to the non-

target. These findings suggest that generation of early frontal P3 could be related to alerting activity of the frontal cortex, while generation of later parietal P3 is related to activation of the temporal-parietal network.

Results obtained from these two experiments are highly consistent with the thesis that a huge positive deflection of ERP with a peak latency of 300-800 ms, and commonly dubbed as P3 (or P300) is not a unitary potential (Polich and Criado, 2006; Polich, 2007), but rather represents a temporal overlap of activities of numerous widely distributed brain areas. Consequently, the P3 may be composed of at least a few constituent subcomponents which reflect distinct cognitive processes. These subcomponents appear to vary in their locus of scalp distribution, magnitude and peak latency as a function of the stimulus context. There are at least two which are commonly accepted, namely the P3a and the P3b. These two components correspond closely to the frontal and parietal P3 distinguished in the first two experiments.

The P3a is a large positive deflection with a relatively short latency and a maximum recorded at frontal-central location. It can be obtained in response to auditory or visual infrequent stimuli presented with physically different frequent stimuli in the passive condition similar to those applied in our second experiment (Jeon and Polich, 2001; Mertens and Polich, 1997). It can also be observed in the active three-stimulus variant of the oddball paradigm, where an additional infrequent non-target stimulus is inserted into a sequence of frequent standard and infrequent target stimuli, as it was done in active condition of the second experiment (Katayama and Polich, 1998; 1999). In both cases no response to those stimuli is required. Short latency of the P3a component as well as its frontal-central distribution support the suggestion that it reflects an alerting process in the frontal cortex, which is elicited while attention is involuntary shifted towards a new stimulus. This effect is observed in the experiments presented in chapters 2 and 3. An early P3a can therefore be linked to the initial attention reallocation occurring as the result of stimulus attribute change. Such a process follows primary sensory processing and stimulus feature mismatch detection. It has been also suggested that P3a can be generally similar to the orienting response.

Similar component can also be measured in response to novel ‘distracter’ stimuli (e.g. dog barks) that are not repeated frequently and are inserted in a series of standards and targets. This component is sometimes referred to as ‘novelty’ P3 (Courchesne, Hillyard and Galambos, 1975; Knight, 1984). There is evidence that P3a and ‘novelty’ P3 are identical phenomenon. Simons and his coworkers (2001) used the original tasks to evoke an auditory P3a (Squires, Squires and Hillyard, 1975) and a ‘novelty’ P3 (Courchesne et al., 1984) and found no differences between these two components. Similar findings were also reported by Polich and Comerchero (2003). These authors compared brain responses to novel and non-novel visual distracters to replicate the original three-

stimulus reports (Courchesne, Hillyard and Galambos, 1975; Courchesne, Courchesne and Hillyard, 1978). Both types of distracter stimuli produced virtually identical P3 with frontal-central distribution. Combs and Polich (2006) obtained identical results using auditory stimuli.

In contrast to this, the P3b (or classical P3) has a more posterior-parietal scalp distribution and a somewhat longer latency than P3a. This component can be regarded as a correlate of target stimulus classification and can be easily recorded in tasks in which some form of controlled response to stimuli is required (Donchin and Coles, 1988; Kok, 2001). This characteristic of P3b component was clearly demonstrated comparing responses measured in passive and active condition in the second experiment. The most popular form of such task is the oddball task, where rare target stimuli are inserted in series of much more frequent standard stimuli of the same modality. The subject is usually asked to notice the presence of target stimulus and to react to it, typically by pressing a button, or just by mental counting. P3 responses with a similar topography can also be generated in a single stimulus task where a single target is randomly presented as in the oddball paradigm, but with the standard stimuli replaced by silence (Polich, Eischen and Collins, 1994; Mertens and Polich, 1997; Strüber and Polich, 2002). An experimental procedure of this kind is used in the first experiment presented in chapter 2. Thus, the P3b component seems to be elicited exclusively by stimuli demanding active controlled processing and subsequent obligatory response. According to this, the P3b has been considered as indexing voluntary attention, in such a way that its amplitude reflects the allocation of attentional resources (Kok, 2001, Wronka et al., 2007), and its peak latency is considered to be related to stimulus evaluation time (Kutas, McCarthy and Donchin, 1977).

### Neural sources of P3 component

Functional distinction between P3a and P3b suggest that both components stem from the activity of different brain regions. This suggestion was touched in the third experiment, in which neural generators of each of the components elicited in the three-stimulus oddball task were identified using the standardized low resolution electromagnetic tomography (sLORETA). The results obtained in this experiment suggested that major sources of the P3a can be localized within the frontal cortex and the anterior cingulate gyrus. This is consistent with many previous reports suggesting that frontal cortex makes a major contribution to the scalp recorded P3a. Specifically, patients with a frontal lesion demonstrate attenuated amplitude of the P3 recorded at frontal sites, while their parietal response can be less affected (Knight, 1984; Yamaguchi and Knight, 1991b; Knight,

Grabowecky and Scabini, 1995). These results are also in line with more recent neuroimaging and ERP studies showing that activity of the frontal cortex can be related to detection of infrequent or alerting stimuli (Potts et al., 1996; McCarthy et al., 1997; Verbaten, Huyben and Kemner, 1997; see also Bocquillon et al. 2011, for review). Similarly, there is evidence from dipole analysis that "novelty" P3 can be linked with prefrontal activity (Mecklinger and Ullsperger, 1995).

In contrast to this, results obtained form the third experiment showed that main sources of the P3b can be located within the superior parietal lobule and the posterior part of the cingulate gyrus. This finding is consistent with the suggestion that neural generators of the P3b are located more posteriorly than the P3a. The more anterior located source for non-target P3 as compared to target P3 was recently reported by Barry and Rushby (2006), using LORETA source localization. It closely corresponds to data obtained from human lesion research. Specifically, P3b amplitude is reduced after brain damage in the temporal-parietal junction (Knight et al., 1989; Yamaguchi and Knight, 1991a; Verleger et al., 1994), which suggests more posterior localization of its neural source when compared to P3a. This hypothesis is also supported by the Halgren and colleagues (1995) findings from intracerebral recording in patients. These authors reported that activity within superior temporal gyrus and hippocampus at about 380 ms post-stimulus may be reflected in the scalp P3b. This is also in line with recent magnetoencephalographic recording and functional imaging studies (Menon et al., 1997; Alho et al., 1998; Li, Wang and Hu, 2009; see also Bocquillon et al., 2011 for review).

**P3 component in relation to fluid intelligence**

Several previous reports suggest that the P3 component can be reliably linked to individual differences in intelligence. Specifically, it was shown that latency of this component is negatively correlated with scores in intelligence tests, which might be interpreted as an indication that the level of cognitive abilities is inversely related to the speed of information processing (Vernon et al., 2000). At the same time, results from studies testing the relationship between P3 magnitude and intelligence are mixed and inconclusive. Some authors have found that P3 amplitude is negatively correlated with intelligence (McGarry-Roberts, Stelmack and Campbell, 1992; Zhang, Caryl and Deary, 1989), while in several other studies a significant correlation in opposite direction has been reported (Alcorn and Morris, 1996; Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002). Thus, it is not obvious how the intensity of the P3 response is related to the level of cognitive abilities. It is even less clear

when one considers the fact that P3 is composed of at least two subcomponents, the P3a and the P3b, reflecting different stages of information processing and having various cortical generators.

The purpose of the fourth experiment (see chapter 5) was to examine the relationship between basic characteristic of both P3 subcomponents, elicited in the active version of the auditory three-tone oddball paradigm, and the psychometrically determined level of cognitive abilities. Additionally, neuronal sources of the effect were specified. It was found that the amplitudes of P3a and P3b components are sensitive to differences in cognitive abilities and that the amplitude is higher for the group scoring higher on Raven APM. The results obtained from this experiment are consistent with findings from several previous studies (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002). It indicates that higher mental abilities, as defined by psychometric intelligence tests, are closely related to a greater ease in voluntary stimulus discrimination reflected in the P3b amplitude. Similar differences were observed for target and non-target stimuli, what might suggest that the relationship between P3b amplitude and intelligence is independent of the stimulus meaning. At the same time, larger P3a amplitude in the group with higher scores on RAPM was also found, which can indicate that higher cognitive abilities are related to more intense initial attention engagements, provoked by the detection of mismatch between the presented stimulus and the passively formed neuronal traces of previous stimuli.

Consistently, intelligence-related differences in scalp recorded P3a were associated with various levels of cortical activities as revealed by source analysis (the standardized low resolution electromagnetic tomography – sLORETA). Stronger frontal activity was observed for the latency window covering the P3a component in the group scoring higher on RAPM. What should be noticed, is that a comparable pattern of differences was obtained for target and non-target stimuli. At the same time the location of brain structures where the effect of intelligence was found corresponds closely to the location of cortical generators of P3a component (Wronka, Kaiser and Coenen, 2012). Similarly, results from source analysis performed for the P3b component reveal differences in the level of parietal cortex activity. A stronger activation of this region was found for the high ability participants. And again, a very similar pattern of differences was observed for target and non-target stimuli. Neural source of these effects were localized within the same group of brain structures, which were previously identified as the generators of P3b component (Wronka, Kaiser and Coenen, 2012).

Similar conclusions can be drawn from the fifth experiment (see chapter 6), where amplitude of P3 component evoked by visual stimuli was compared in two groups differentiated by the RAPM score. A significantly larger P3 was recorded for subjects

scoring higher on Raven's test. This result leads to the implication that the observed effect of intelligence, reflected in a greater magnitude of the P3 subcomponents measured in subjects with higher fluid intelligence, can be obtained using various paradigms and at least two different modalities. Thus, it is reasonable to conclude that a higher fluid intelligence is closely linked to more intense attention engagement and resource allocation, which probably determines a more precise detection of relevant stimuli and a better adjustment of subsequent response to these stimuli.

Findings from these two experiments obviously demonstrate that processes related to the initial stage of attention engagement, as indexed by P3a, as well as the later stimulus evaluation and classification, reflected in P3b, are more intense in subjects scoring higher on classic intelligence tests. The effects of mental abilities observed in these studies could be related to differences in frontal and parietal brain regions. Similar findings were recently reported by other authors (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002). In all these studies a higher amplitude of P3 response was measured from subjects scoring higher on test of cognitive abilities.

It is worth to notice that the relationship between the level of cognitive abilities and basic characteristics of P3 component can be mediated by at least two specific factors, namely cortical thickness and stability of brain potentials. Specifically, Fjell and Walhovd (2007) reported significant correlation between amplitude of P3a and P3b and the intraindividual variability of these components. In other words, the more variable the P3 response from trial to trial is, the lower is the mean amplitude of this component. Concurrently, the intra-individual variability of P3 responses was also negatively related to verbal and performance intelligence, as well as to cortical thickness in the precentral gyrus and the temporoparietal junction. These findings indicate that a high intelligence can be associated with a more stable brain responses reflected in less variable P3a and P3b potentials. This relationship can be linked to higher cortical thickness in frontal and parietal regions. A significant positive relationship between cognitive abilities and overall cortical grey matter volume was also demonstrated by Walhovd and collaborators (Walhovd et al. 2005).

The above mentioned findings are in line with results from a study of Grey, Chabris and Braver (2003), who found that the level of cognitive abilities could be closely linked to the activity within the frontal and the parietal lobes. They also reported that the relationship between Raven's score and accuracy in an n-back task can almost entirely depend on activation in these brain areas. This is also consistent with Haier and colleagues (2004) report that cognitive abilities can be related to variation in brain structures within the frontal and the parietal lobes.

The role of the frontal and the parietal cortices was also emphasized by Prabhakaran et al. (1997), who compared fMRI activity recorded when subjects have performed distinctly g-loaded tasks. The findings reported by these authors suggest that the prefrontal cortex, together with the superior parietal region, is highly relevant for fluid reasoning. A similar conclusion was also drawn by Duncan et al. (2000), who measured PET responses in two differently g-loaded tasks. They reported that a higher brain activity in the task was highly correlated with standard measures of fluid intelligence when compared to a task with lower g-load. Significant effects were observed for brain areas located in the lateral and the medial frontal cortex, the parietal lobe, and the occipital cortex. The effect was additionally confirmed by Lee et al. (2006), who found a greater bilateral activity in the lateral prefrontal, the medial frontal and the parietal areas when a complex high g-loaded task was compared with a much simpler one. Findings from these experiments indicate the relevance of the frontal and the parietal cortical regions in tests reflecting fluid intelligence.

These findings are also in line with data reported from studies on abstinent alcoholics (Begleiter and Porjesz, 1995; Hada et al., 2000; 2001; Pfefferbaum et al., 1991, Porjesz, Begleiter and Garozzo, 1980; Porjesz et al., 1987; Porjesz and Begleiter, 1996). Major cognitive problems observed in long-term alcoholics are associated with incorrect attention functioning. There is evidence from neuroimaging studies indicating that alcoholics exhibit general cortical and specifically frontal lobe deficits compared to control subjects, perhaps because of excessive alcohol consumption. Begleiter and coworkers (1980) have reported a serious cortical atrophy in alcoholics. At the same time alcoholics without cortical atrophy exhibited larger P3b amplitudes in comparison to alcoholics with substantial cortical atrophy. Main areas of the brain where cortical volume losses can be observed in alcoholics, are localized in the diencephalon, caudate nucleus, dorsolateral frontal cortex, parietal cortex (Jernigan et al., 1991). Moreover, significantly less prefrontal grey matter was found in older alcoholics in comparison to younger alcoholics, while the difference in white matter volume was especially severe in the prefrontal regions (Pfefferbaum et al., 1997). There is also evidence that local cerebral metabolic rate for glucose bilaterally in the medial frontal area, is decreased for alcoholics compared to normal control subjects. The severity of the clinical neurological impairments in these alcoholics significantly correlated with the degree of hypometabolism in the medial frontal region (Gilman et al., 1996). Furthermore, the local cerebral metabolic rate for glucose was significantly decreased in the medial frontal cortex in alcoholics, with a reliable relationship between glucose metabolic rate in the medial frontal region and the Wisconsin Card Sorting Test performance (Adams et al., 1993), which is a well-established index of prefrontal neuropsychological function (Shimamura, 1995). Taken together with ERP studies showing a diminished P3 responses in alcoholics, it is reasonable to suppose

that alcoholics demonstrate a considerable dysfunction in frontal cortex and especially prefrontally. These results suggest that cognitive impairment in alcoholics (Eckardt et al., 1988; Goldman and Goldman, 1988; Sanders, Nixon and Parson, 1989; Tamkin and Dolenz, 1990; Tarbox, Conners and McLaughlin, 1986), may stem from fundamental neuroanatomical variables that contribute to the P3 generation.

### Parieto-Frontal Network as a neural basis of fluid reasoning

Taking all these findings together it can be concluded that there is strong relationship between the level of fluid intelligence and the efficiency of fronto-parietal network. Results from experiments presented in the thesis indicate that brain areas relevantly linked with the general intelligence and fluid reasoning are primarily located in the parietal and frontal lobes. One of their most important function is to integrate information among various parts of the nervous system. Most of the brain regions which constitute this parieto-frontal network are closely related to elementary cognitive processes, such as working memory and attention. Relationship between fluid intelligence and efficiency of the attention system can be studied using the measurement of P3 component as it was revealed in two experiments presented in this book (see chapter 5 and 6). Findings from these experiments suggest that high level of fluid intelligence is associated with stronger P3 response. This response is generated by the widely distributed brain areas (see chapter 4). Obviously, brain structures located in the frontal and the parietal lobes, which can be involved in P3 generation, can be associated with various different psychological processes. According to this, the main attributes of fluid intelligence cannot be connected with single part of the brain or a single characteristic of the nervous system functioning, but rather are associated with a network of brain structures and functions distributed throughout the cortex. People scoring higher on IQ tests have cortical networks that operate more accurately and quickly in comparison to those of less intelligent individuals. Therefore the differences between individuals scoring higher and lower on the psychometric tests of fluid intelligence can be observed in any behavioral tasks which have strong connection to functions of the parieto-frontal network. Fluid intelligence can be interpreted as the product of a flexible, adaptive neural system. More specifically, it can be proposed that intelligent individuals have dynamic neural networks that alter their functioning in order to accommodate tasks demands, and parallel, cortical regions that work effectively to perform a specific function (Newman and Just, 2005). Results form neuroimaging studies have found that neural synchrony becomes more precise when tasks become more difficult. Moreover, this

synchrony is positively related to task performance and scores on intelligence tests (Newman and Just, 2005; Stankov, 2005).

The assumption that fluid intelligence can be associated with the activity of the fronto-parietal network is based on converging evidence from many cognitive neuroimaging and electroencephalographic studies that varied in their operational definitions of intelligence and their methods of assessing it. Early studies using positron emission tomography (PET) found that individuals who obtained high IQ scores had brains that expended less energy, and consequently consumed less glucose, than the brains of individuals with lower IQ scores (Haier et al., 1988; 1992). However, reports from many later studies are inconsistent with Haier's hypothesis. Larson and his coworkers (1995) contrasted PET data gathered on participants who solved two working memory tasks differing in difficulty. They found that individuals scoring higher on Raven's test exhibit higher cortical metabolic rates than participants in the lower IQ group. The obtained effect was most evident for frontal and parietal regions. Similar results were also reported by Gray, Chabris and Braver (2003) employing an event-related fMRI technique to test whether general fluid intelligence can be mediated by brain regions that support attentional control. Magnitude of event-related activity in the lateral prefrontal cortex (PFC), the dorsal anterior cingulate, and the cerebellum was positively correlated with RAPM scores in this study. Similarly, positive relation between the level of cognitive abilities and indexes of brain activity was also reported by Lee at al. (2006). The role of the frontal and parietal regions was also emphasized Duncan et al (2000) and Prabhakaran et al (1997).

Contradiction between findings reported by Haier and his colleagues (1998; 1992) and those obtained by other groups (Gray, Chabris and Braver, 2003; Larson et al., 1995; Lee et al., 2006) can be explained by major differences among experimental procedures and measurement techniques used in those studies. For example, Haier and his coworkers (1988, 1992) have measured brain activity with PET using $^{18}$fluoro-2-deoxyglucose (FDG), which has an uptake time of 30 minutes. In contrast to this, event-related fMRI was used to asses brain activity in other experiments (Gray, Chabris and Braver, 2003; Lee et al., 2006). This technique enable to measure brain activity in relatively short time intervals (few seconds). Results from these experiments enable to link the higher fluid intelligence with enhanced short term phasic response of the fronto-parietal network. At the same time, findings from early research of Haier et al. (1988, 1992) suggest that the aggregate 30-minute brain activity is negatively correlated with IQ scores. Therefore it is reasonable to propose that high fluid intelligence is associated with stronger short-term activation of the fronto-parietal network which represents the more efficient information processing. Due to the greater efficiency of this network, high

intelligent individuals are able to perform the task faster and commiting less errors, which in turn require less effort and can be linked with overall lower long-term activation.

It is worth to notice that findings form studies testing the relationship between basic characteristic of P3 component of the ERP and psychometric measures of fluid intelligence are also in line with results from neuroimaging research. Two experiments presented in chapter 5 and 6 have shown that higher level of cognitive abilities can be associated with greater amplitude of P3a and P3b subcomponents. Similar results were previously reported by other authors (Bazana and Stelmack, 2002; Beauchamp and Stelmack, 2006; DePascalis, Varriale and Matteoli, 2008; Fjell and Walhovd, 2003; 2007; Sculthorpe and Stelmack, 2009; Walhovd and Fjell, 2002). Moreover, results from source analysis presented in chapter 5 indicate that IQ-related differences in scalp recorded EEG can be linked with activity within the frontal and the parietal cortices, the same group of brain structures which were previously identified as the generators of P3b component (Wronka, Kaiser and Coenen, 2012).

Taking all these findings together it is reasonable to conclude that despite procedural differences among experiment in which various methods of brain activity recording have been used, there was reassuring consistency across studies in the brain regions associated with individual differences in performance on general intelligence and reasoning tasks. The brain network closely related to fluid reasoning consist of the lateral frontal cortex, the medial frontal cortex with the anterior cingulate gyrus as its relevant part, lateral parietal cortex extending to parieto-temporal junction, and the posterior part of the cingulate gyrus and adjacent medial parietal areas. Differences in activity observed in this network can be therefore postulated as the neural basis of fluid intelligence.

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**SUMMARY**

The present work refers to the problem of the relationship between cognitive abilities, defined as fluid intelligence, and their neuronal backgrounds. There is consensus that intelligence is closely related to the efficiency of brain functioning. This idea has roots in Spearman's theory of general intelligence, and is later expanded by Cattell and Horn. Modern psychologists commonly believe that brain activity plays a central role in intelligence, but there is no commonly accepted theory in which this role is accurately described.

In Chapter 1, several theories associating intelligence with specific features of brain functioning, are outlined. Most of them are based on the supposition that basic properties of cognitive abilities, which are closely linked to intelligence, can be observed on the brain level. Due to this, differences in brain processes connected to these abilities can reflect the biological basis of intelligence. According to this, several hypotheses have been proposed as a possible variable enabling explanation of the individual differences in mental abilities. Speed of neural transmission can be one of the hypotheses . Another concept, which has been applied in the explanation of the biological basis of intelligence, is Hendricksons' idea that efficiency of brain transmission can be solely the source of variation in human cognitive abilities. At the empirical level, this phenomenon can be reflected in the complexity of Event-Related Potentials (ERP), measured as the 'string length' index (or 'string measure'). There has also been a suggestion that differences in fluid intelligence can be related to brain efficiency, reflected in various levels of energy consumption or engagement of different number of neurons. According to this hypothesis, a high fluid intelligence can be linked to a more economically functioning brain. However, as it is presented in the introductory chapter, results from studies exploring the problem of the relationship between fluid intelligence and brain activity are inconclusive. This chapter ends with the suggestion that the neuronal basis of fluid reasoning can be explained by different efficiency of attention mechanism, which can be reflected in the amplitude of the P3 component.

In the following chapters electrophysiological studies testing basic characteristic of frontal and parietal P3 subcomponents are described. The main scientific question in the first experiment (Chapter 2) was, how the basic features of the auditory P3 subcomponents would be affected by the simultaneous presentation of irrelevant visual stimuli, involuntarily engaging attention. Subjects were presented with a series of neutral tones, either alone or accompanied by the simultaneous exposition of a neutral pictures in two different sessions. In the first session, tones demanded no further cognitive activity from the subjects (passive or 'ignore' session), while in the second session subjects were instructed to count the tones (active or 'count' session). ERP responses in the 'ignore'

session revealed only a small P3-like component over the parietal and frontal cortex, however, when the auditory stimuli co-occurred with the visual stimuli, an increased frontal activity was observed. This effect was interpreted as the reflection of a more intensive involuntary attention shift, provoked by earlier visual stimulation. Moreover, it was found that the cognitive load, caused by the 'count' instruction, resulted in an evident P3, with maximal amplitude over the parietal locations. This effect was smaller when auditory stimuli were presented on the visual background. These findings support the thesis that the P3 component reflects the process of attention resources allocation.

The study described in Chapter 3 was designed to compare the basic characteristics of the P3 subcomponents elicited in passive and active versions of the 3-stimulus oddball paradigm. Results show that the magnitude of the frontal P3 response is determined by the relative perceptual distinctiveness among stimuli. The amplitude of the frontal component was found to be larger for the stimuli more deviated from the standard in both passive and active tasks. Moreover, amplitude of this component was influenced by the strength of attentional focus. Significantly larger responses were obtained in the active session compared to its passive counterpart. Apparent parietal P3 responses were only obtained in the active condition. The amplitude of this component was larger for the target than for the non-target, but both demonstrated parietal maxima. These findings suggest that the generation of the early frontal P3 could be related to alerting activity of the frontal cortex. Moreover, the generation of a later parietal P3 could be linked with the activation of the temporo-parietal network, observed when neuronal model of perceived stimulation and attentional trace are compared.

The main aim of the study presented in Chapter 4 was to define the scalp topography of the two subcomponents of the P3 elicited in a three-stimulus oddball paradigm, and to identify their cortical generators using the Standardized Low Resolution Electromagnetic Tomography (sLORETA). Major neural generators of the P3a have been found to be localized within the frontal cortex and the anterior cingulate gyrus. In contrast to this, the P3b, showing maximal amplitude at parietal locations, was larger for stimuli demanding response than for the rare non-target. Major sources of the P3b included the superior parietal lobule and the posterior part of the cingulate gyrus. These findings are in line with the hypothesis that the P3a is related to alerting activity during the initial allocation of attention, while the P3b is related to the activation of the posterior network.

The experiment reported in Chapter 5 was designed to examine the relationship between psychometric intelligence measured with the Raven's Advanced Progressive Matrices (RAPM) and event-related potentials (ERP), using a 3-stimulus oddball task. Subjects scoring higher on RAPM exhibited larger amplitudes of the P3a component. An additional analysis using the Standardized Low Resolution Electromagnetic Tomography (sLORETA) has revealed that this effect can be related to stronger activity within the frontal cortex

and the cingulate gyrus. High intelligence can also be linked with a greater P3b response and stronger activity within the parietal cortex and the posterior cingulate gyrus. It has been concluded that processes related to the initial stage of attention engagement, as indexed by the P3a, as well as later stimulus evaluation and classification, reflected in the P3b, are more intense in subjects scoring higher on RAPM. Therefore, the quality of mental abilities can be related to differences of the activity in frontal and parietal brain regions.

The study described in Chapter 6 was designed to establish the relationship between fluid intelligence, measured with the Raven's Advanced Progressive Matrices (RAPM), and the patterns of brain activity in a task engaging attention. Subjects were presented with the Ericksen's Flanker Task. Simultaneously, ERP responses were recorded. The obtained results suggest that a higher level of fluid intelligence could be linked to a more efficient detection of the response conflict. This concept was in a more differentiated N2 amplitude, when compared to the individuals with lower intelligence level. Additionally, a larger amplitude of the P3 component was measured from subjects scoring higher on RAPM. The effects on the N2 and P3 indicate a presumable link between the activities of the frontal and parietal lobes. Moreover, they may suggest that these activities are closely related to the efficiency or quality of cognitive abilities reflected in the psychometrically evaluated intelligence. Therefore, the main finding of this thesis implies that a high level of cognitive abilities is closely related to an efficient functioning of the attention mechanism.

The results obtained from all these experiments are discussed in Chapter 7. The experimental outcomes support the thesis that the frontal and parietal cortical regions constitute the neuronal basis of human fluid intelligence. This is consistent with findings from previous electrophysiological and neuroimaging studies, suggesting that the brain activity within these regions differs significantly between subjects scoring 'low' and 'high' on tests measuring fluid intelligence. It has also been previously suggested that the same brain parts form the network are involved in attention mechanism. Due to this, it is proposed that the efficiency of the attention functioning can be closely related to fluid intelligence.

**SAMENVATTING**

Het in deze thesis gepresenteerde werk gaat over de kwestie hoe cognitieve vaardigheden, gedefinieerd als 'fluid' intelligentie, tot stand komen door de werking van een onderliggend neuronaal substraat. Er is consensus dat intelligentie te maken heeft met de efficiëntie van het functioneren van het brein, welk idee al wortels heeft in Spearman's theorie inzake algemene intelligentie, een theorie die verder uitgewerkt is door Cattell en Horn. Hedendaagse psychologen zijn inderdaad van mening dat de activiteit van het brein een centrale rol vervult in intelligentie, maar er is nog geen algemeen geaccepteerde theorie die deze rol adequaat beschrijft.

In Hoofdstuk 1 worden diverse theorieën inzake het verband tussen intelligentie en specifieke breinkenmerken, besproken. De meeste zijn gebaseerd op de veronderstelling dat basale eigenschappen van cognitieve vaardigheden, die te maken hebben met intelligentie, op het neuronale breinniveau gevormd worden. Dat betekent dat verschillen in breinprocessen die ten grondslag liggen aan cognitieve vaardigheden, de biologische basis van intelligentie zouden kunnen weerspiegelen. Dienovereenkomstig zijn verscheidene hypothesen opgesteld met mogelijke variabelen die individuele verschillen in mentale vaardigheden zouden kunnen verklaren. De snelheid van de neurale transmissie zou een van deze variabelen kunnen zijn. Een ander concept dat van toepassing zou kunnen zijn ter verklaring van de biologische basis van intelligentie, is Hendricksons' idee dat efficiëntie in breintransmissie de belangrijkste bron is die de variatie in menselijke cognitieve vaardigheden verklaart. Empirisch kan dit fenomeen zichtbaar worden gemaakt in de complexiteit van 'Event-Related Potentials' (ERP), bijvoorbeeld gemeten als de 'string length' index. Een andere suggestie is dat verschillen in 'fluid' intelligentie gerelateerd zou kunnen worden aan breinefficiëntie, meetbaar op diverse niveaus van energie consumptie, of in de betrokkenheid van aantallen neuronen. Volgens deze hypothese kan een hogere 'fluid' intelligentie gekoppeld worden aan een meer economisch werkend brein. Maar de uitkomsten van studies naar het probleem van de relatie tussen 'fluid' intelligentie en breinactiviteit zijn geen van alle overtuigend. Het hoofdstuk eindigt met de suggestie dat verschillen in 'fluid' intelligentie verklaard zouden kunnen worden met verschillen in efficiëntie van attentiemechanismen. Deze zouden tot uitdrukking gebracht kunnen worden in de amplitude van de P3 component van de ERP.

De verdere hoofdstukken bevatten electrofysiologische studies met een beschrijving van de basale karakteristieken van frontale en parietale subcomponten van de P3. De wetenschappelijke vraag in het eerste experiment (Hoofdstuk 2) is hoe basale kenmerken van auditieve P3 subcomponenten beïnvloed kunnen worden door de gelijktijdige presentatie van irrelevante visuele stimuli, die toch onbewust aandacht vragen. Aan proefpersonen is een serie neutrale tonen gepresenteerd, hetzij alleen, hetzij vergezeld

van neutrale plaatjes, in twee verschillende sessies. In de eerste sessie vereisen de tonen geen verdere cognitieve activiteit van de subjecten (de passieve of 'ígnore' conditie), terwijl in de tweede sessie de subjecten de instructie gekregen hebben om de tonen te tellen (de actieve of 'count' sessie). De ERP responsies in the 'ignore' sessie laten een kleine P3-achtige component over de parietale en frontale cortex zien, maar wanneer echter de auditieve stimuli samen met de visuele stimuli getoond zijn, dan kan een toegenomen frontale activiteit geobserveerd worden. Dit effect is geïnterpreteerd als een reflectie van een meer intensieve onwillekeurige verschuiving in attentie, geïnduceerd door de visuele stimuli. Bovendien is gevonden dat de cognitieve lading, veroorzaakt door de 'count' instructie, resulteert in een duidelijke P3, met een maximale amplitude over de parietale locaties. Dit effect is kleiner dan wanneer de auditieve stimuli gepresenteerd zijn op een visuele achtergrond. Deze bevindingen steunen de veronderstelling dat de P3 component een reflectie is van het proces dat resources verzorgt voor het attentiemechanisme.

De studie beschreven in Hoofdstuk 3 is opgezet om de basale karakteristieken van de P3 subcomponenten, opgewekt in de passieve en actieve versies van het 3-stimulus 'oddball' paradigma, te onderzoeken. De resultaten tonen aan dat de grootte van de frontale P3 bepaald wordt door het verschil in het perceptuele onderscheid tussen stimuli. De amplitude van de frontale component wordt groter voor stimuli die meer en meer afwijkend zijn van de standaard, zowel in passieve als in actieve taken. Voorts wordt de amplitude van deze component beïnvloed door de sterkte van de focus van attentie. Significant grotere responsies zijn verkregen in actieve vergeleken met passieve sessies. Duidelijke, parietale P3 responsies zijn slechts verkregen in de actieve conditie. De amplitude van deze component is groter voor de target dan voor de non-target, maar beide vertonen maxima over de parietale locaties. Deze bevindingen suggereren dat het genereren van de vroege frontale P3 gerelateerd zou kunnen worden aan de attenderende activiteit van de frontale cortex. Bovendien kan het genereren van de latere parietale P3 gekoppeld worden aan de activering van het temporo-parietale netwerk. Deze activering komt tot uiting wanneer het neuronale model van de stimulatie en het spoor van de attentie met elkaar vergeleken worden.

Het doel van de studie van Hoofdstuk 4 was, ten eerste, om de scalp topografie van de twee subcomponenten van de P3, opgewekt met het drie-stimulus paradigma te bepalen, en, ten tweede, om de corticale generatoren van deze componenten vast te stellen via de 'Standardized Low Resolution Electromagnetic Tomography' (sLORETA) methode. Belangrijke neurale generatoren van de P3a blijken aanwezig te zijn in de frontale cortex en in de gyrus cingulatus anterior. In tegenstelling hiermee vertoont de P3b, een maximale amplitude over de parietale locaties en is groter voor responsie-vragende target stimuli dan voor non-target stimuli. Belangrijke bronnen voor de P3b zijn de

superieure parietale lobule en het posterieure gedeelte van de gyrus cingulatus. Deze resultaten zijn in overeenstemming met de hypothese dat de P3a te maken heeft met attenderende activiteiten tijdens de initiële allocatie van attentie, terwijl de P3b gerelateerd is aan de activering van het posterieure netwerk.

In het experiment beschreven in Hoofdstuk 5 staat de relatie tussen de psychometrische intelligentie, bepaald met de 'Raven's Advanced Progressive Matrices' (RAPM) schaal, en de 'Event-Related Potentials' (ERP), verkregen met het 3-stimulus oddball taak paradigma, centraal. Subjecten die hoger scoren op de RAPM vertonen een grotere amplitude op de P3a component. Een additionele analyse met sLORETA levert op dat dit effect komt door een sterkere activiteit in de frontale cortex en de gyrus cingulatus. Een hoge intelligentie kan ook gekoppeld worden aan een grotere P3b responsie met een sterkere activiteit in de parietale cortex en de posterieure gyrus cingulatus. Geconcludeerd is dat processen die te maken hebben met het initiële stadium van de betrokkenheid van attentie, zoals aangegeven wordt door de P3a, evenals door latere stimulus evaluatie en classificatie te zien in de P3b, meer intens zijn in subjecten die hoger scoren op de RAPM. De kwaliteit van mentale vaardigheden kan daardoor gerelateerd worden aan verschillen in activiteit tussen frontale en parietale breingebieden.

Het onderzoek van Hoofdstuk 6 betreft het verband tussen 'fluid' intelligentie, gemeten met de Raven's Advanced Progressive Matrices (RAPM), en patronen in breinactiviteit tijdens een attentievragende taak. 'Ericksen's Flanker Task' is gepresenteerd aan proefpersonen, terwijl tegelijkertijd de ERP responsies zijn afgeleid. De resultaten suggereren dat een hoger niveau van intelligentie in verband gebracht kan worden met een meer efficiënte detectie van het responsieconflict. Dit komt tot uitdrukking in een meer gedifferentieerde N2 amplitude, vergeleken met individuen met een lager intelligentie niveau. Daarbij komt dat een hogere amplitude van de P3 component gemeten is bij subjecten die hoger scoren op de RAPM. De effecten op N2 en P3 wijzen op een waarschijnlijk verband tussen de activiteiten van frontale en parietale gebieden. Dit zou voorts kunnen suggereren dat deze activiteiten nauw gerelateerd zijn aan de efficiëntie of kwaliteit van cognitieve vaardigheden, zoals die tot uiting komen in de psychometrisch vastgestelde intelligentie. De belangrijke vondst van deze thesis is dan ook de implicatie dat een hoog niveau van cognitieve vaardigheden gerelateerd is aan een efficiënt functionerend attentiemechanisme.

De resultaten van alle experimenten zijn bediscussieerd in Hoofdstuk 7. De uitkomsten ondersteunen de veronderstelling dat frontale en parietale corticale gebieden de neuronale basis van 'fluid' intelligentie vormen. Dit is consistent met bevindingen van eerdere electrofysiologische en neuroimaging studies, die aangeven dat de breinactiviteit in deze gebieden significant verschilt tussen subjecten die 'hoog' en 'laag' scoren bij testen die 'fluid' intelligentie meten. Ook al eerder is gesuggereerd dat deze

breingebieden een netwerk vormen dat nauw betrokken is bij attentiemechanismen. Al met al wordt voorgesteld dat de efficiëntie van de attentiefunctie direct betrokken is bij het niveau van ‘fluid’ intelligentie .

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## Curriculum Vitae

Eligiusz Wronka was born in Kępno, Poland on 13$^{th}$ of November 1971. In 1991 he finished the secondary school in Rybnik. From 1991 till 1995 he studied psychology at the Institute of Psychology of Jagiellonian University (UJ) in Kraków. In 1995 he obtained his M.A. degree and was awarded PhD scholarship at the Jagiellonian University. After five years he obtained the Phd degree at the Jgiellonian University in 2000. Since 2002 within the cooperation between Radboud Univeristy in Nijmegen (RU) and UJ he has been working at his PhD thesis. His supervisors were Prof. dr A.M.L. Coenen from RU and Prof dr Jan Kaiser form UJ.

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